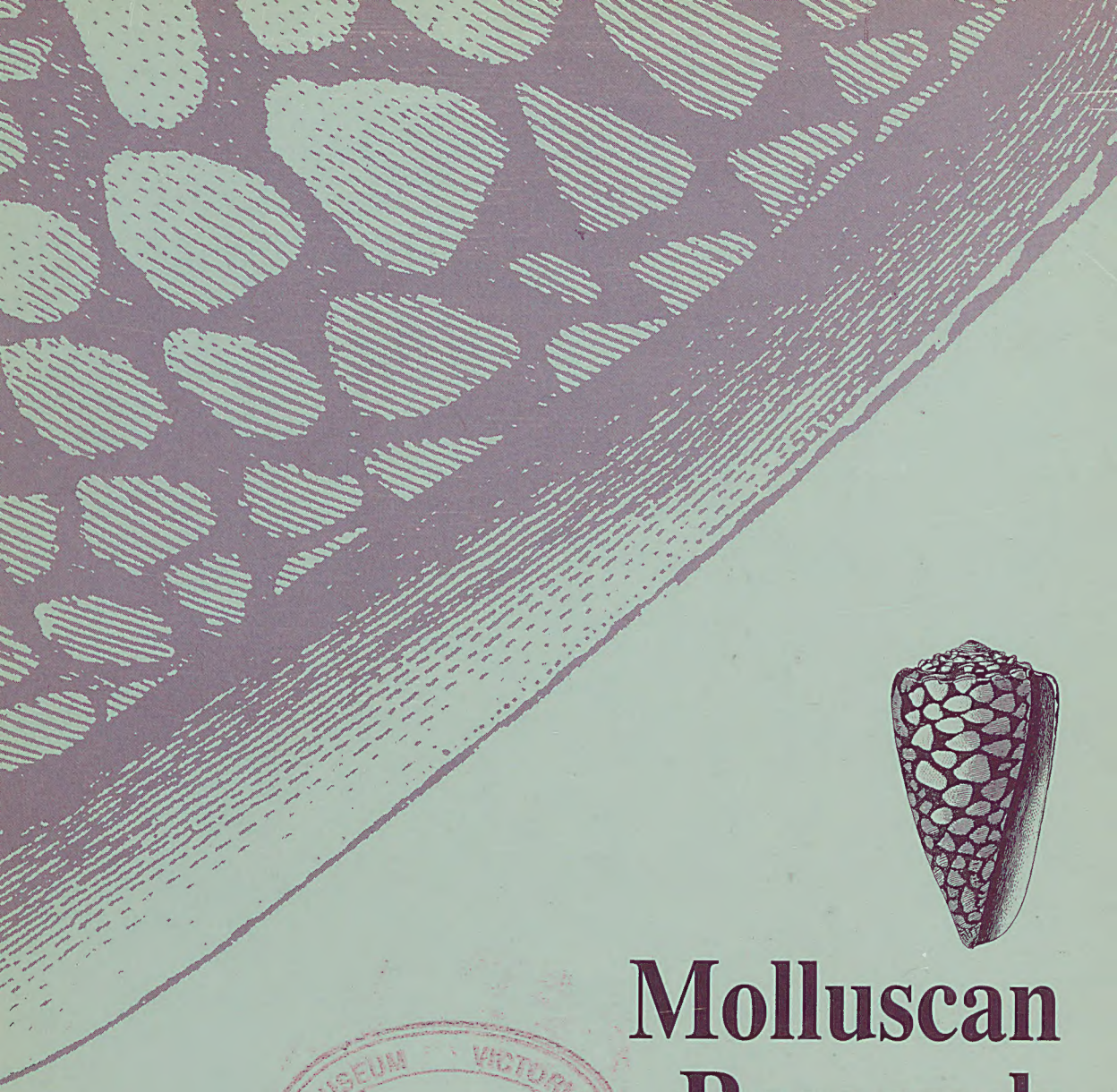

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MOLLUSCAN RESEARCH

Volume 19, Number 2 19 November 1998

CONTENTS

E.S. Upatham , P. Wangsomnuk , M. Kruatrachue , Y. P. Chitramvong & V. Reutrakul
Acute toxicity of a plant molluscicide, *Brassaia actinophylla* on *Indoplanorbis exustus* and non-target organisms 1

M. Kruatrachue , E. S.Upatham , P. Wangsomnuk , P. Sretarugsa , & Y. Chitramvong
Ultrastructural changes in the digestive system of *Indoplanorbis exustus* (Gastropoda : Planorbidae) exposed to the molluscicides, niclosamide and *Brassaia actinophylla* 15

L. Triantafillos , S. Donnellan & A. J. Butler
Population genetic structure of the muricid gastropod *Lepsiella vinosa* in Gulf St Vincent, South Australia 31

H.H. Dijkstra & J. Knudsen
Some Pectinoidea (Mollusca: Bivalvia: Propeamussiidae, Pectinidae) of the Red Sea 43

D.S. Brown
Freshwater snails of the genus *Gyraulus* (Planorbidae) in Australia: the taxa of Tasmania 105

Book Review
J.Stanisic
Bivalves of Australia, Volume 2 155

Acute toxicity of a plant molluscicide, *Brassaia actinophylla* on *Indoplanorbis exustus* and non-target organisms

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Abstract

A total of 50 different plant species of 22 families was investigated for molluscicidal activity against *Indoplanorbis exustus*. Twenty-one species (42%) demonstrated molluscicidal activity. The crude water extract of *Brassaia actinophylla* showed the best result with 24 hr. LC50 and LC90 values of 23.73 and 32.11 mg/l, respectively. The control group of snails exposed to niclosamide showed 24 hr. LC50 and LC90 values of 0.009 and 0.01 mg/l, respectively. The 24 hr. LC50 and LC90 values of the crude water extract of *B. actinophylla* on two species of fish, namely, *Puntius gonionotus* and *Poecilia reticulata* were 47 and 55 mg/l, and 85 and 111 mg/l, respectively. Concerning the crustacea, *Moina macrocopa* and *Macrobrachium rosenbergii*, the 24 hr. LC50 and LC90 values of the crude water extract of *B. actinophylla* were 258 and 861 mg/l, and 141 and 181 mg/l, respectively.

Key words : acute toxicity, plant molluscicide, *Brassaia actinophylla*; *Indoplanorbis exustus*; *Puntius gonionotus*; *Poecilia reticulata*; *Moina macrocopa*; *Macrobrachium rosenbergii*.

Introduction

In recent years, a large number of plants in tropical and temperate regions of the world have been tested on snails for molluscicidal activity (Lemma *et al.*, 1984; Adewunmi, 1984; Ahmed *et al.*, 1984; Evans *et al.*, 1986; Farnsworth *et al.*, 1987; Geerts *et al.*, 1991; Zhou *et al.*, 1993). Certain plant species had shown to be very active, such as *Phytolacca dodecandra* (Lemma *et al.*, 1984), *Swartzia madagascariensis* (Sarda *et al.*, 1986) and *Tetrapleura tetraptera* (Adewunmi, 1984). These plants are used as extracts or are placed directly into snail habitats. However, most of the plant species were collected in Brazil, Egypt, Nigeria, Puerto Rico and Sudan. To the best of our knowledge, there is virtually no information on the testing of plant species with molluscicidal activity in Thailand. Since Thailand is a tropical country and has a rich biodiversity of plant species, it is worthwhile to investigate the native plant species that show promising molluscicidal activity. Hence, the primary objective of the present study was to select the native plant species with molluscicidal activity against the schistosomiasis-mediating snails, *Indoplanorbis exustus* (Deshayes).

Only a few plant molluscicides have been studied beyond their target molluscicidal effects. The investigations on the effects of extracts of various plant species on non-target organisms such as *Daphnia*, snails, mosquito larvae, earthworms, fish and birds have been done in an attempt to predict hazards to non-target biota (Lemma, 1970; Lemma & Yau, 1974; Squire *et al.*, 1989; Lambert *et al.*, 1991; Monkiedje *et al.*, 1991; Pretorius *et al.*, 1991; Geerts *et al.*, 1991, 1994; Brackenberry & Appleton, 1997a, 1997b; Brackenberry *et al.*, 1997). However, a few plant species have been subjected to mammal or long-term toxicological

studies (W.H.O 1983), such as *P. dodecandra* and *Ambrosia maritima* which have undergone mammal and mutagenic testing (Lambert *et al.*, 1991; Geerts *et al.*, 1994). *Apodytes dimidiata* underwent similar toxicity assessment (excluding mutagenicity and acute inhalation) and proved to be less toxic to mammals, worms and fish (Brackenberry & Appleton, 1997a). Another plant molluscicide, *Agave attenuata* has proved to be non-toxic to crop plants, invertebrates, fish and mammals (Brackenberry & Appleton, 1997b). Laboratory tests of toxicity to non-target organisms have often been carried out with small fish and microcrustaceans (Lemma & Yau, 1974; Squire *et al.*, 1989; Monkiedje *et al.*, 1991; Geerts *et al.*, 1991). Based on these considerations, two species of fish *Puntius gonionotus* (young) and *Poecilia reticulata* (adult) and two species of crustaceans *Moina macrocopa* (adult) and *Macrobrachium rosenbergii* (young), were selected. Hence, another objective of the present investigation was to study the toxicity of selected plant molluscicide on these non-target organisms.

Materials and Methods

Animals

Snails used in this study were laboratory-bred *Indoplanorbis exustus*, which were cultured in aerated glass aquaria with mud as substrate, and fed with lettuce leaves in the Center for Applied Malacology, Department of Biology, Faculty of Science, Mahidol University, Bangkok, Thailand.

Screening for promising plant molluscicides

A total of 50 different plant species with potential molluscicidal activity was selected from a list of plants already studied by Kloos & McCullough (1987), Farnsworth *et al.* (1987), and NAPRALERT data base. Plant materials were collected from different parts of Thailand. They were authenticated at Khon Kaen University, where voucher specimens were deposited (voucher number, No. P 1-40).

To prepare a crude water extract, the plant was dried in a hot air oven at 40-45°C. The dried leaves were ground into powder in a blender. The powdered leaves were passed through an 80-mesh sieve and extracted with dechlorinated tap water overnight using the method described by Adewunmi (1984).

Preliminary screening

For preliminary screening, the crude water extract of plants was employed. Laboratory-bred offsprings of *I. exustus* with the shell diameters of 13-16 mm were exposed to crude water extract of powdered leaves of different plant species. Toxicity experiments were performed using the method of Adewunmi (1984) and the standard procedure for laboratory screening of W.H.O. (1971). Twenty-five adult snails were kept in a plastic aquarium containing 3 l of dechlorinated tap water for 24 hr. After this period, five snails were transferred to glass containers that contain 225 ml crude water extract of plant at different concentrations (25, 50, 100, 200, 500, 1000 mg/l). They were exposed under 40-watt fluorescence ceiling lights at 25-27°C. The exposure time was 24 hr. and the recovery period was 48 hr. to determine for LC50 and LC90. Control groups

were kept in dechlorinated tap water without any treatment. A range of extraction time, the weight of plant material to dechlorinated water volume ratios, and the number of dead snails were recorded.

Definitive screening

Plants that had shown high potential molluscicidal activity in any of the preliminary tests were tested for definitive screening. The method for definitive screening followed the same procedures as that for preliminary screening. Each set of experiments was replicated four times. After the recovery period the mortality of the snails was recorded. The LC50 and LC90 values were computed from a dose - mortality response curve with a 24 hr. exposure and a 48 hr. recovery period. Confidence limits of the LC50 and LC90 values were calculated by probit analysis (Finney, 1971) and a computer probit analysis program developed by Raymond (1987).

In the present study, the crude water extract of *Brassaia actinophylla* has shown the best LC50 and LC90 values.

Toxicity tests of Brassaia actinophylla and niclosamide on Indoplanorbis exustus

In order to compare the toxicity of *B. actinophylla* in crude water extract or methanol extract, the powdered leaves of *B. actinophylla* were extracted with absolute methanol in a Soxhlet apparatus, then evaporated under reduced pressure using an evaporator. The resultant viscous oil was allowed to stand in a vacuum desiccator until it crystallised.

The crystals of *B. actinophylla* were dissolved with dechlorinated tap water and administered to the snails, *I. exustus*.

The Bayluscide, or niclosamide was used as a standard molluscicide to compare with plant molluscicide for 24 hr. LC50 and LC90 values. Niclosamide used was 70% wettable powder.

Testing for 24 hr. LC50 and LC90 values of *B. actinophylla* in both crude water extract of powdered leaves and crystalline solid from methanol extract, and those of niclosamide, employed similar procedures to those described previously in preliminary and definitive screening. The concentrations of niclosamide used in preliminary screening were 0.01, 0.02, 0.03, 0.04 and 0.05 mg/l.

Toxicity tests of Brassaia actinophylla on non-target organisms

The non-target organisms, two species of fish *Puntius gonionotus* (30-45 mm in length) and *Poecilia reticulata* (15-25 mm in length), and two species of crustaceans *Moina macrocopa* (adult) and *Macrobrachium rosenbergii* (65 days old juvenile) were obtained and acclimatized for at least seven days prior to testing. The toxicity test for 24 hr. LC50 and LC90 values of these organisms exposed to the crude water extract and methanol extract of *B. actinophylla* followed the same procedures described previously for the snails, *I. exustus*. All bioassay tests were conducted without aeration or renewal of water, at a room temperature of 25-27 °C. All control groups were exposed to dechlorinated tap water.

The 24 hr. and 48 hr. LC50 and LC90, 95% confidence intervals and slopes of probit line were determined for each test group by the method described by Finney (1971) and a computer program probit analysis developed by Raymond (1987).

Results

Screening for promising plant molluscicides

The definitive screening results obtained from the crude water extract of 50 plant species of 22 families are shown in Table 1. Among 50 plant species, 4 (8%) of which showed high molluscicidal activity (LC90 <100 mg/l), 9 (18%) had moderate activity (101 < LC90 < 500 mg/l), 8 (16%) had very low activity (501 < LC90 < 1000 mg/l) and 29 (58%) had no molluscicidal activity (LC90 >1000 mg/l or no snail mortality). Twenty-one species (42%) produced extracts which demonstrated molluscicidal activity.

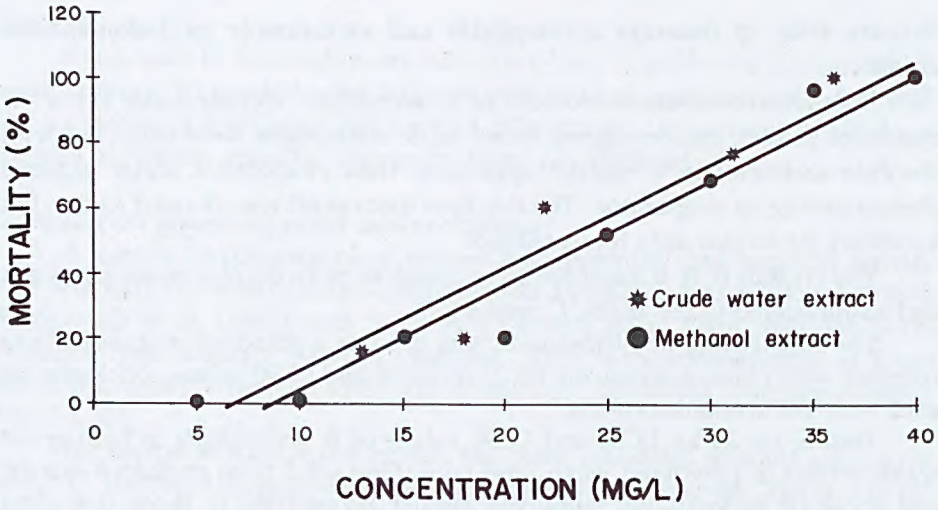

Figure 1. The dose - response curves of snails, *I. exustus* exposed to crude water and methanol extracts of *B. actinophylla.*

Acute toxicity of Brassaia actinophylla and niclosamide

The mortality of *Indoplanorbis exustus* increased with the concentration of molluscicides after 24 hr. exposure and 48 hr. recovery. In niclosamide used as a reference standard, the LC50 and LC90 values were 0.009 and 0.01 mg/l, respectively (Table 2). In crude water extract of *B. actinophylla,* the LC50 and LC90 values were 23.73 and 32.11 mg/l, respectively, whereas in methanol extract, the LC50 and LC90 values were 23.40 mg/l and 35.48 mg/l, respectively (Table 2). No dead snails were observed in control groups. The dose - response curves of *I. exustus* exposed to *B. actinophylla* and niclosamide are shown in Figs. 1 and 2, respectively.

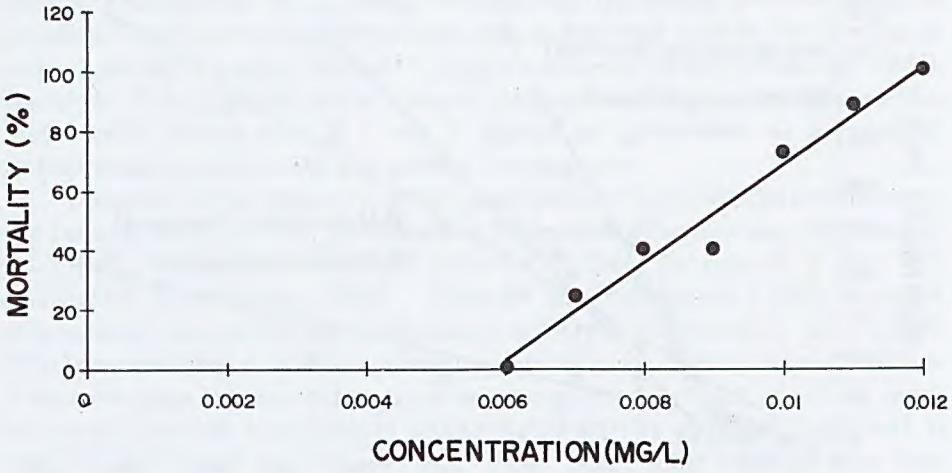

Figure 2. The dose-response curve of snails, *I. exustus* exposed to niclosamide.

Toxicity tests on non-target organisms

The acute toxicity of *B. actinophylla* to non-target organisms, fish and crustaceans is shown in Table 3. The dose-response curves of fish, *Puntius gonionotus* and *Poecilia reticulata*, and of crustaceans, *Moina macrocopa* and *Macrobrachium rosenbergii* exposed to crude water extract and methanol extract of *B. actinophylla*, are shown in Figs. 3 and 4, respectively.

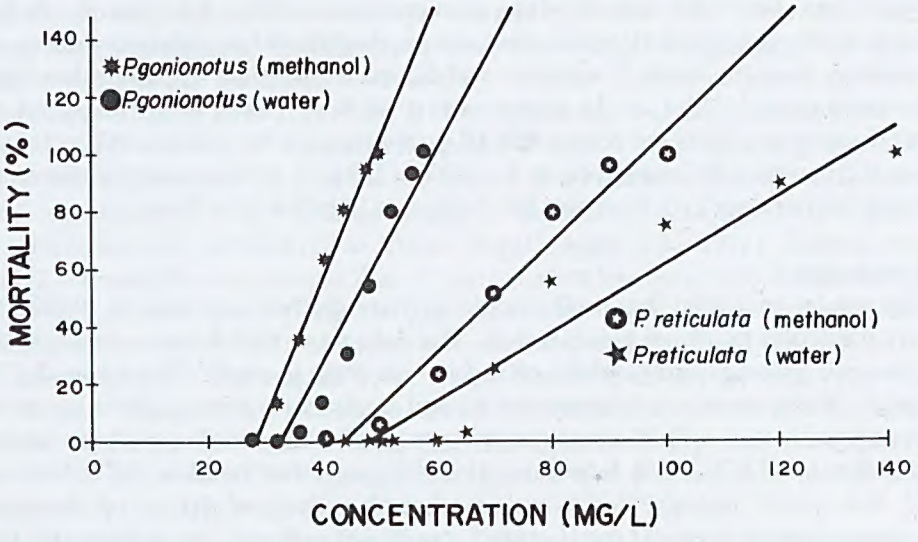

Figure 3. The dose-response curves of fish, *P. gonionotus* and *P. reticulata* exposed to crude water and methanol extracts of *B. actinophylla*.

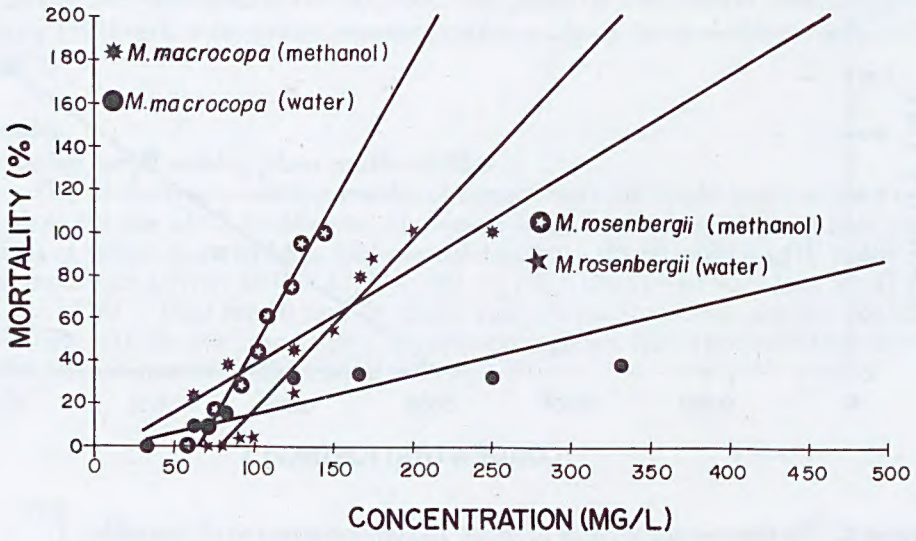

Figure 4. The dose-response curves of crustaceans, *M. macrocopa* and *M. rosenbergii* exposed to crude water and methanol extracts of *B. actinophylla*.

In the snails *I. exustus*, the crude water extract produced a slightly higher mortality rate than methanol extract of *B. actinophylla* (Figs. 3,4). In fish and crustaceans, the methanol extract was more toxic (Figs. 3,4). The results also showed that *I. exustus* was more sensitive to *B. actinophylla* than non-target organisms. Fish were more sensitive than crustaceans (Figs. 3,4; Table 3). At the 24 hr. LC90, young fish (*P. gonionotus)* and crustaceans (*M. rosenbergii)* were more sensitive than the adult *P. reticulata* and *M. macrocopa*. It is apparent that high concentrations of the crude water extract of *B. actinophylla* are required to produce toxic effects on young fish (*P. gonionotus*, 24 hr. LC50 = 141 g/l) and adult crustacean (*M. macrocopa*, 24 hr. LC50 = 258 g/l). These concentrations are much higher than toxicity levels for *I. exustus* (24 hr. LC50 = 23 mg/l).

Discussion

The results indicated that molluscicidal activity did not appear to be limited to any particular family of plants tested. The data show that *Brassaia actinophylla, Reissantia grahamii* and *Gardenia obtusifolia* are toxic to snails. The 24 hr. LC50 and LC90 values of crude water extract and methanol extract of dried leaves of these plants are within the standard range of being molluscicidally active (100 mg/l, W.H.O., 1983). Sarda *et al.* (1986) showed that the 24 hr. LC100 values of the crude water extract and methanol extract of fruits of *Swartzia madagascariensis* were 30 mg/l and 25 mg/l, respectively. In addition, in the laboratory experiments, *Tetrapleura tetraptera* was effective against *Bulinus globosus* (Morelet), *Lymnaea columella* Say, *L. natalensis* Krauss, *Biomphalaria pfeifferi* (Krauss), *B. glabrata* (Say) and *Physa waterloti* Germain at concentrations

less than 10 mg/l for methanol extracts, and less than 50 mg/l for crude water extracts (Adewunmi *et al.*, 1982). Moreover, the crude water extract of powdered berries of endod (*Phytolacca dodecandra*) had a 24 hr. LC90 value at only 17.46 mg/l against *Bulinus truncatus serinicus* (Jickeli) (Lemma, 1970). Therefore, *B. actinophylla* in the present study, whose 24 hr. LC90 value of the crude water extract was 32.11 mg/l, should be considered as a potential molluscicidal plant and requires further investigation.

Variations in the amount of active principle and molluscicidal activity have also been reported in many plant species (Ndamba & Chandiwana, 1989; Geerts *et al.*, 1991; Vasiliades *et al.*, 1986; Farnsworth, 1966; Farnsworth *et al.*, 1987; Adewunmi & Sofowora, 1980). Ndamba & Chandiwana (1989) reported geographical variation in the molluscicidal activity in *P. dodecandra*. Geerts *et al.* (1991) reported that *Ambrosia maritima* in populations contained large quantities of sesquiterpene lactones before the plants were distributed for use in the field. Moreover, there are variations of molluscicidal activity of plants cultivated in different environments (Vasiliades *et al.*, 1986). Some of the reported variations in toxicity in plants studied by different investigators, are probably due to differences in collection methods, plant varieties and ecotypes occurring in different climates, habitats, temperature, amount of rainfall, soil and extraction solvent (Farnsworth, 1966; Vasiliades *et al.*, 1986). Adewunmi & Sofowora (1980) reported that the reason for the absence of toxicity in some plants from a genus known to contain molluscicide compound could be because there was a chemical race deficiency, or that the content of this constituent was too low to be toxic at the time of collection.

The 24 hr. LC90 values of crude water extract of *B. actinophylla* against *Indoplanorbis exustus* snails and fish, *Puntius gonionotus* and *Poecilia reticulata* were 32, 55 and 111 mg/l, respectively. This result shows that *B. actinophylla* at the concentration that kills *I. exustus*, does not kill the fish. However, such concentration might kill the fish if they were exposed for a longer period of time due to subacute or sublethal toxic action. In other species of plants studied, *P. dodecandra* killed 90% of the fish at the molluscicidal concentrations used in the field and was also very toxic to mammals (Kloos & McCullough, 1987). The LC50 and LC90 values of crude water extract of *A. maritima* that killed *Lebistes reticulatus* (guppy) were 650 and 690 mg/l, respectively, 2-10 times doses used as molluscicide in the field (70 to 300-400 mg/l) (Alard *et al.*, 1991). These show that *B. actinophylla* is more toxic than *A. maritima* but less toxic than *P. dodecandra*.

The results of toxicity testing of *B. actinophylla* on crustaceans, *Macrobrachium rosenbergii* and *Moina macrocopa* showed that the LC90 values of *B. actinophylla* for crustaceans were much higher (5-25 times) than that for *I. exustus*. This is very similar to endod (*P. dodecandra*) whose LC100 value against snails was 31-50 times lower than that against shrimps (Gebremedhin *et al.*, 1994). The crude water extract of *A. maritima* also was not toxic to *Daphnia magna* with the LC90 more than 2000 mg/l (Alard *et al.*, 1991).

It can be concluded that *B. actinophylla* is toxic to *I. exustus* but less toxic to the species of fish and crustaceans studied. Further research is needed to discover whether *B. actinophylla* can kill snails under local field conditions; can kill enough snails when applied by simple means; can reduce schistosomiasis

transmission significantly; and can be cost-effective. The present study, aiming at finding high-potential molluscicides, also reported on the species of non-molluscicidal and low-potential molluscicidal plants, as well as identifying plants which might yield molluscicidal extracts. The results presented here may be useful in minimizing duplication of work and reducing unnecessary costs for other investigators.

References

Adewunmi, C.O. 1984. Water extract of *Tetrapleura tetraptera* : an effective molluscicide for the control of schistosomiasis and fascioliasis in Nigeria. *Journal of Animal Protection Research* **4:** 73-80.

Adewunmi, C.O., Adesina, S.K. & Marquis, V.O. 1982. On the laboratory and field trials of *Tetrapleura tetraptera. Bulletin of Animal Health and Production in Africa* **30:** 89-94.

Adewunmi, C.O. & Sofowora, E.A. 1980. Preliminary screening of some plant extracts for molluscicidal activity. *Planta Medica* **39:** 57-65.

Ahmed, E.M., Bashir, A.K. & El Kheir, Y.M. 1984. Investigations of molluscicidal activity of certain Sudanese plants used in folk-medicine. Part IV. *Planta Medica* **50(1):** 74-77.

Alard, F., Geerts, S. and Triest, L. 1991. Toxicite d' *Ambrosia maritima* L., plant molluscicide, sur les organismes aquatiques noncibles. *Toxicon* **29:** 745-750.

Brackenbury, T.D. & Appleton, C.C. 1997a. Acute toxicity evaluation of the plant molluscicide, *Apodytes dimidiata* (Icacinaceae), to *Eisenia fetida* (Oligochaeta) and *Oreochromis mossambicus* (Cichlidae) in South Africa. *Acta Tropica* **63:** 1-14.

Brackenbury, T.D. & Appleton, C.C. 1997b. A comprehensive evaluation of *Agave attenuata,* a candidate plant molluscicide in South Africa. *Acta Tropica* **68:** 201-213.

Brackenbury, T.D., Appleton, C.C. & Thurman, G. 1997. Mammal toxicity assessment of the plant molluscicide, *Apodytes dimidiata* (Icacinaceae), in South Africa. *Acta Tropica* **65:** 155-162.

Evans, N.A., Whitfield, P.J. Squire, B.J., Fellows, L.E., Evans, S.V. & Millott, S.M. 1986. Molluscicidal activity in the seeds of *Milletia thonningii* (Leguminosae : Papillionoideae). *Transaction of the Royal Society of Tropical Medicine and Hygiene* **80:** 451-453.

Farnsworth, N.R. 1966. Biological and phytochemical screening of plants. *Journal of Pharmaceutical Sciences* **55:** 225-276.

Farnsworth, N.R., Henderson, T.O. & Soejarto, D.D. 1987. Plants with potential molluscicidal activity. pp. 131-204. In: Mott, K.E. ed. *Plant Molluscicides.* John Wiley & Sons Ltd., Chichester.

Finney, D.J. 1971. Probit Analysis. 3rd ed. Cambridge University Press, Cambridge.

Gebremedhin, G., Adewunmi, C.O., Becker, W., Agbedahunsi, J.M. & Dorfler, G. 1994. Hirudinicidal activities of some natural molluscicides used in schistosomiasis control. *Journal of Ethnopharmacology* **41:** 127-132.

Geerts, S., Belot, J., Sabbe, F., Triest, L. & Sidhom, M. 1991. *Ambrosia maritima*: effects on molluscs and non-target organisms. *Journal of Ethnopharmacology* **30:** 1-2.

Geerts, S., Van Blerk, K. & Triest, L. 1994. Effect of *Ambrosia maritima* on *Anopheles stephensi* and *Aedes aegypti. Journal of Ethnopharmacology* **42:** 7-11.

Kloos, H. & McCullough, F.S. 1987. Plant with recognized molluscicidal activity. pp. 45-108. In : Mott, K.E. ed. *Plant Molluscicides.* John Wiley & Sons Ltd., Chichester.

Lambert, J.D.H., Temmink, J.H.M., Marquis, J., Pankhurst, R.M., Lugt, C.H.B., Lemich, E., Wolde-Yohannes, L. & De Savigny, D. 1991. Endod-safety evaluation of plant molluscicides. *Regional Toxicology and Pharmacology* **14:** 189-210.

Lemma, A. 1970. Laboratory and field evaluation of the molluscicidal property of *Phytolacca dodecandra*. *Bulletin of the World Health Organization* **42:** 597-617.

Lemma, A. & Yau, P. 1974. Studies on the molluscicidal properties of Endod *(Phytolacca dodecandra)*. II Comparative toxicity of various molluscicides to fish and snails. *Ethiopian Medical Journal* **12:** 109-113.

Lemma, A., Heyneman, D. & Silangwa, S.M. 1984. *Phytolacca dodecandra* (Endod). Tycooly International Publishing Ltd., Dublin.

Monkiedje, A., Anderson, A.C. & Englande, A.J. 1991. Acute toxicity of *Phytolacca dodecandra* (Endod-S) and niclosamide to snails, *Schistosoma mansoni* cercariae, *Tilapia* fish, and soil microorganisms. *Environmental Toxicology and Water Quality* **6:** 405-413.

Ndamba, J. & Chandiwana, S.K. 1989. The geographical variation in the molluscicidal potency of *Phytolacca dodecandra* (Endod) berries in Zimbabwe. *Tropical and Geographical Medicine* **40:** 30-48.

Pretorius, S.J., Joubert, P.H., Scott, A.H. & Gourie, T.G. 1991. The molluscicidal properties of *Apodytes dimidiata* (Icacinaceae). *Journal of Tropical Medicine and Hygiene* **94:** 159-165.

Raymond, M. 1987. Probit Analysis Program : Presentation de un programme d'analyse log-probit pour micro-ordinatinnateur. *Cahiers OSTROM, Serie Entomologie Medicale et Parasitologie* **22(2):** 117-121.

Sarda, R.K., Chhabra, S.C. & Minjas, J.N. 1986. Laboratory observations on the molluscicidal properties of *Swartzia madagascariensis* (Leguminosae). *Journal of Ethnopharmacology* **15:** 211-213.

Squire, B.J., Pilcher, M.W., Whitfield, P.J., El-Banhawy, M.A. & Rashed, R.M.A. 1989. Fish toxicity of the molluscicidal seeds of *Millettia thonningii* (Leguminosae : Papillionoideae) : impact on *Tilapia nilotica/ aura* hybrids and *Ctenopharyngodon idella. International Journal of Environmental Science* **33:** 93-98.

Vasiliades, G., Diaw, O.T. & Roberge, G. 1986. Note sur la comparaison des propietes molluscicides d' *Ambrosia maritima* (Egypte) et d' *Ambrosia senegalensis* (Senegal). *Revue de Elevage et de Medicine Veterinaire des Pays Tropicaux* **39:** 341-343.

W.H.O. 1971. Annex 1 : Definitive laboratory screening-standard methods. *Meeting of Directors of Collaboration Laboratories on Molluscicide Testing and Evaluation.* WHO/SCHISTO/71.6, pp. 26-29.

W.H.O. 1983. Report of the scientific working group on plant molluscicides. *Document No. TDR/SCH-SWG* **(4) 83.3,** Geneva.

Zhou, X., Upatham, E.S., Kruatrachue, M. & Sretarugsa, P. 1993. Effects of niclosamide and *Eucalyptus camaldulensis* on *Biomphalaria glabrata,* the snail intermediate host of *Schistosoma mansoni. Journal of the Science Society of Thailand* **19:** 117-128.

Table 1. Summary of snail toxicity study and phytochemical screening.

Family/Genus/Species	Part [a] tested	LC50 (mg/l)	LC90 (mg/l)	Collection area
ACANTHACEAE				
Asystasia gangetica T. Anders.	l	>1000	>1000	Khon Kaen
Ruellia tuberosa Linn.	l	-	-	Bangkok
AMARANTHACEAE				
Gomphrena celosioides Mart.	l	-	-	Khon Kaen
G. globosa Linn.	l	-	-	Bangkok
ANNONACEAE				
Anomianthus dulcis Sincl.	l	925	>1000	Chiang Mai
Melodorum fruticosum Lour.	l	>1000	>1000	Bangkok
Miliusa velutina Hook. f. & Th.	l	>1000	>1000	Chiang Rai
Orophea enterocarpa Maing. ex Hook. f. & Th.	l	-	-	Narathiwat
Rouwenhoffia siamensis Schaeff.	l	101	225	Bangkok
APOCYNACEAE				
Allamanda cathartica Linn.	l	92	198	Khon Kaen
Nerium indicum Mill.	l	648	>1000	Bangkok
Plumaria alba Linn.	l	-	-	Khon Kaen
ARALIACEAE				
Brassaia actinophylla Endl.	l	23	35	Khon Kaen
CAESALPINACEAE				
Cassia angustifolia Vahl.	l	>1000	>1000	Khon Kaen
CELASTRACEAE				
Reissantia grahamii (Wright)	l	34	62	Chachoengsao
COMPOSITAE				
Eupatorium odoratum Linn.	l	163	570	Nakhon Ratchasima
Gynura pseudo-china DC. var. *hispida* Thv.	ap	-	-	Pathum Thani
Pluchea indica Less.	l	23	35	Khon Kaen
Solidago polyglossa DC.	l	>1000	>1000	Pathum Thani
Spilanthes acmella (Linn.) Merr.	l	-	-	Khon Kaen
Synedrella nodiflora (Linn.) Gaertn.	l	142	246	Khon Kaen
Tagetes erecta Linn.	l	>1000	>1000	Pathum Thani
Tridax procumbens Linn.	l	-	-	Khon Kaen
Vernonia cinerea (Linn.) Less.	l	-	-	Khon Kaen
Wedelia trilobata Hitchc.	l	84	134	Bangkok
Zinnia elegans Jacq. (Zannia)	l	-	-	Pathum Thani
CUCURBITACEAE				
Momordica charantia Linn.	ap	427	710	Khon Kaen
Trichosanthes integrifolia Kurz.	l	>1000	>1000	Pathum Thani

Family/Genus/Species	Part [a] tested	LC50 (mg/l)	LC90 (mg/l)	Collection area
EUPHORBIACEAE				
Acalypha indica Linn.	l	>1000	>1000	Bangkok
Euphorbia hirta Linn.	l	682	781	Khon Kaen
Jatropha integerrima Jacq.	l	811	979	Bangkok
Calophyllum teysmonis Mig.	l	254	434	Narathiwat
C. calaba Linn. var *bracteatum* (Wright) Stevens	l	217	567	Narathiwat
LABIATAE				
Hyptis suaveolens (L.) Poit.	l	701	970	Khon Kaen
LEGUMINOSAE (PAPILIONOIDEAE)				
Crotolaria pallida DC.	l	675	>1000	Khon Kaen
MALVACEAE				
Sida acuta Burm. f.	l	>1000	>1000	Khon Kaen
Urena lobata Linn.	l	579	814	Khon Kaen
MILIACEAE				
Sandoricum koetjape (Burm. f.)Merr.	l	285	391	Bangkok
NYCTAGINACEAE				
Boerhavia diffusa Linn.	l, fl	650	946	Khon Kaen
OLEANDRACEAE				
Nephrolepis falcata (Cav.) C. Chr.	l	-	-	Bangkok
PIPERACEAE				
Piper samentosum Roxb. ex Hunt.	l	-	-	Khon Kaen
RHAMNACEAE				
Ventilago harmandina Piere.	l	-	-	Ratchaburi
RUBIACEAE				
Gardenia erythroclada Kurz.	l	-	-	Chiang Mai
G. obtusifolia Roxb.	l	39	74	Chiang Mai
SAPINDACEAE				
Nephelium hypoleucum Kurz.	l	92	141	Nakhon Ratchasima
Adenosoma indianum (Lour.) Merr.	l, fl	-	-	Nakhon Ratchasima
Angelonia salicariifolia Humb & Bonpl.	l	129	245	Pathum Thani
SOLANACEAE				
Solanum aculeatissimum Jacq.	l	-	-	Bangkok
VERBENACEAE				
Volkameria fragans Vent.	l	185	330	Khon Kaen
Stachytarpheta indica Linn. Vahl.	l	-	-	Khon Kaen

a : l = leaf, ap = aerial part, fl = flower, - = no snail mortality.

Table 2. Toxicity of niclosamide and *B. actinophylla* in adult snails *I. exustus*.

Molluscicide	24 hr. exposure time LC50 (mg/l)	LC90 (mg/l)
Niclosamide		
LC : estimated by Probit analysis	0.009	0.010
95% confidence limits	0.0083-0.0091	0.0106-0.0124
Slopes of probit line	11.45 ±1.44	11.45 ± 1.44
Brassaia actinophylla		
Crude water extract		
LC : estimated by Probit analysis	23.73	32.11
95% confidence limits	21.08-29.36	29.32-36.77
Slopes of probit line	8.54 ± 1.17	8.54 ± 1.17
Methanol extract		
LC : estimated by Probit analysis	23.40	35.48
95% confidence limits	21.449-25.310	32.061-41.233
Slopes of probit line	7.10 ± 0.92	7.10 ± 0.92

Table 3. Acute toxicity of *B. actinophylla* to non-target organisms

B. actinophylla leaves	LC50 (mg/l)		LC90 (mg/l)	
	24 hr.	48 hr.	24 hr.	48 hr.
Fish				
***P. gonionotus* (young)**				
Crude water extract				
LC : estimated by Probit analysis	47	43	55	48
95% confidence limits	46-48	42-44	53-57	47-50
Slopes of probit line	18.94 ±1.78	26.03 ± 2.94	18.94 ± 1.78	26.03 ± 2.94
Methanol extract				
LC : estimated by Probit analysis	38	35	46	40
95% confidence limits	37-39	34-36	44-48	38-42
Slopes of probit line	16.82 ± 1.62	23.38 ± 2.75	16.32 ± 1.62	23.38 ± 2.35
***P. reticulata* (adult)**				
Crude water extract				
LC :estimated by Probit analysis	85	71	111	79
95% confidence limits	78-93	70-73	96-131	76-83
Slopes of probit line	11.00 ± 1.70	9.43 ± 3.80	11.00 ± 1.70	29.43 ± 3.80
Methanol extract				
LC : estimated by Probit analysis	69	59	86	70
95% confidence limits	66-71	57-61	82-91	67-75
Slopes of probit line	13.39 ± 1.38	17.04 ± 2.09	13.39 ± 1.38	17.04 ± 2.09
Crustacea				
***M. macrocopa* (adult)**				
Crude water extract				
LC : estimated by Probit analysis	258	76	861	306
95% confidence limits	161-413	52-112	306-2446	157-601
Slopes of probit line	2.45 ± 0.62	2.12 ± 0.39	2.45 ± 0.62	2.12 ± 0.39
Methanol extract				
LC : estimated by Probit analysis	106	48	211	131
95% confidence limits	84-134	35-67	142-319	82-213
Slopes of probit line	4.28 ± 0.75	2.95 ± 0.47	4.28 ± 0.75	2.95 ± 0.47
***M. rosenbergii* (young)**				
Crude water extract				
LC : estimated by Probit analysis	141	86	181	130
95% confidence limits	133-150	80-93	166-199	115-148
Slopes of probit line	11.81 ± 1.27	7.16 ± 0.72	11.81 ± 1.27	7.16 ± 0.72
Methanol extract				
LC : estimated by Probit analysis	101	77	132	92
95% confidence limits	96-105	75-79	122-142	89-95
Slopes of probit line	10.95 ± 1.07	16.73 ± 1.51	10.95 ± 1.07	16.73 ± 1.31

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Ultrastructural changes in the digestive system of *Indoplanorbis exustus* (Gastropoda : Planorbidae) exposed to the molluscicides, niclosamide and *Brassaia actinophylla*

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Abstract

The adult snails, *Indoplanorbis exustus* were exposed to the synthetic molluscicide, niclosamide, and the crude - aqueous extract of *Brassaia actinophylla* at the LC50 concentrations (0.009 mg/l and 23.73 mg/l, respectively) for 24 hours. The results showed relatively similar ultrastructural changes in the digestive system of snails exposed to niclosamide and *B. actinophylla*. The general cytological alterations that occurred in the epithelia of esophagus, intestine and digestive gland were the formation of blebs, increased fusion of vacuoles, infolding and thickening of basal lamina, formation of myelin-like figures, degranulation and dilation of rough endoplasmic reticulum, swelling of mitochondria and cristae, and an increase in mucus production. Most of these reactions were more severe in snails treated with *B. actinophylla* than those exposed to niclosamide.

Key words : *Indoplanorbis exustus*, niclosamide, *Brassaia actinophylla*, digestive system

Introduction

There are a relatively few publications concerning ultrastructural changes of the digestive system in gastropods exposed to molluscicides (Adewunmi & Ogbe, 1986; Triebskorn, 1989; 1991; Triebskorn & Künast, 1990; Bourne *et al.*, 1991; Bode *et al.*, 1996). The most extensive studies have been done on slugs such as, *Deroceras reticulatum* (Muller) (Triebskorn, 1989; 1991; Triebskorn & Künast, 1990), where it was reported that molluscicides produced cytological changes in the general outline of cells and in their apical and basal surfaces. The columnar cells of the digestive tract were greatly elongated, and often gaps opened between the epithelial cells and the underlying muscle and nerve tissues (Triebskorn, 1989; Triebskorn & Künast, 1990). Changes at the cell apices included reduction of microvilli, formation of surface blebs and production of a hyaline surface coat overlying the microvilli or cilia (Triebskorn & Künast, 1990). The most striking changes in the basal surface of the cells were development of cell extensions, thickening of the basement membrane, and development of gaps between the epithelium and the basement membrane (Triebskorn, 1989; Triebskorn & Künast, 1990; Bourne *et al.*, 1991).

The most typical cytological changes in the cytoplasm were degranulation and dilation of rough endoplasmic reticulum, formation of membrane whorls, disorganization of Golgi cisternae, intensified fusion of vacuoles, swelling of mitochondria and reduction of cristae, and reduction of storage products (Triebskorn, 1989; 1991; Triebskorn & Künast, 1990). In the nucleus, karyolysis, reduction of heterochromatin, dilation of nuclear envelope and formation of crystalline inclusions were reported (Triebskorn & Künast, 1990).

Most of the ultrastructural studies on cytological changes of the digestive system as results of molluscicides have concentrated only on stylommatophoran slugs and one basommatophoran snail, *Biomphalaria glabrata* (Say) (Bode *et al.*, 1996). Thus, the present electron microscopic study was designed to investigate different cellular responses to a synthetic molluscicide (niclosamide) and a plant extract (*Brassaia actinophylla*) in the digestive system of the freshwater pulmonate, *Indoplanorbis exustus* (Deshayes), the snail intermediate host of *Schistosoma spindale* Montgomery.

Materials and methods

Laboratory-bred, *I. exustus*, with a shell diameter of 1.5-1.8 cm, were used. Batches of thirty snails each were exposed to niclosamide and crude - aqueous extract of *B. actinophylla* at the LC50 concentrations (0.009 mg/l and 23.73 mg/l, respectively) for 24 hours (Upatham *et al.*, in press). The control group consisting of another 30 snails, was subjected to aged tap water.

After the exposure, ten snails from each group were sacrificed. They were relaxed with menthol crystals for 30 minutes and their shells were removed. The organs of the digestive system, esophagus, stomach and intestine, were dissected out and prepared for transmission electron microscope (TEM), viz. first fixed in 2.5% glutaraldehyde in 0.1 M phosphate buffer (pH 7.4) at 4°C for 2 hours, washed in the same buffer and postfixed in 1% OsO_4 in 0.1 M phosphate buffer for 2 hours. The specimens were dehydrated through a graded series of ethanol and embedded in Araldite 502 epoxy resin. Semithin sections were cut with glass knives and stained with methylene blue. Ultrathin sections were cut with a diamond knife, stained with uranyl acetate and lead citrate, and examined with a Hitachi H300 transmission electron microscope operating at 75 KV.

Results

Esophagus

In control snails, the esophagus epithelium consists of two cell types, ciliated columnar cell (columnar storage cell) and mucus-secreting goblet cell (mucus cell) (Fig.1A). The columnar cells bear both microvilli and cilia on the apex (Fig.1B). They contain numerous mitochondria, numerous glycogen rosettes (Fig. 1B), regular membranes of rough endoplasmic reticulum (RER) and Golgi apparatus. The nuclei are rich in heterochromatin and occupy the middle to basal region of the cell. The mucus cells are characterized by conspicuous RER with spacious lumen, mucus vacuoles and glycogen rosettes (Fig.1C). The nuclei are located at the basal region. The infoldings of basal surfaces of both cell types are small, and the basement membrane is very thin (Fig.1D).

The columnar storage cells of both niclosamide and *B. actinophylla* intoxicated snails are still crowded with glycogen granules but the glycogen rosettes are no longer visible (Fig. 2A). There are degranulation and dilation of RER (Fig.2B). No conspicuous alteration was observed in the Golgi apparatus and mitochondria (Fig.2A).

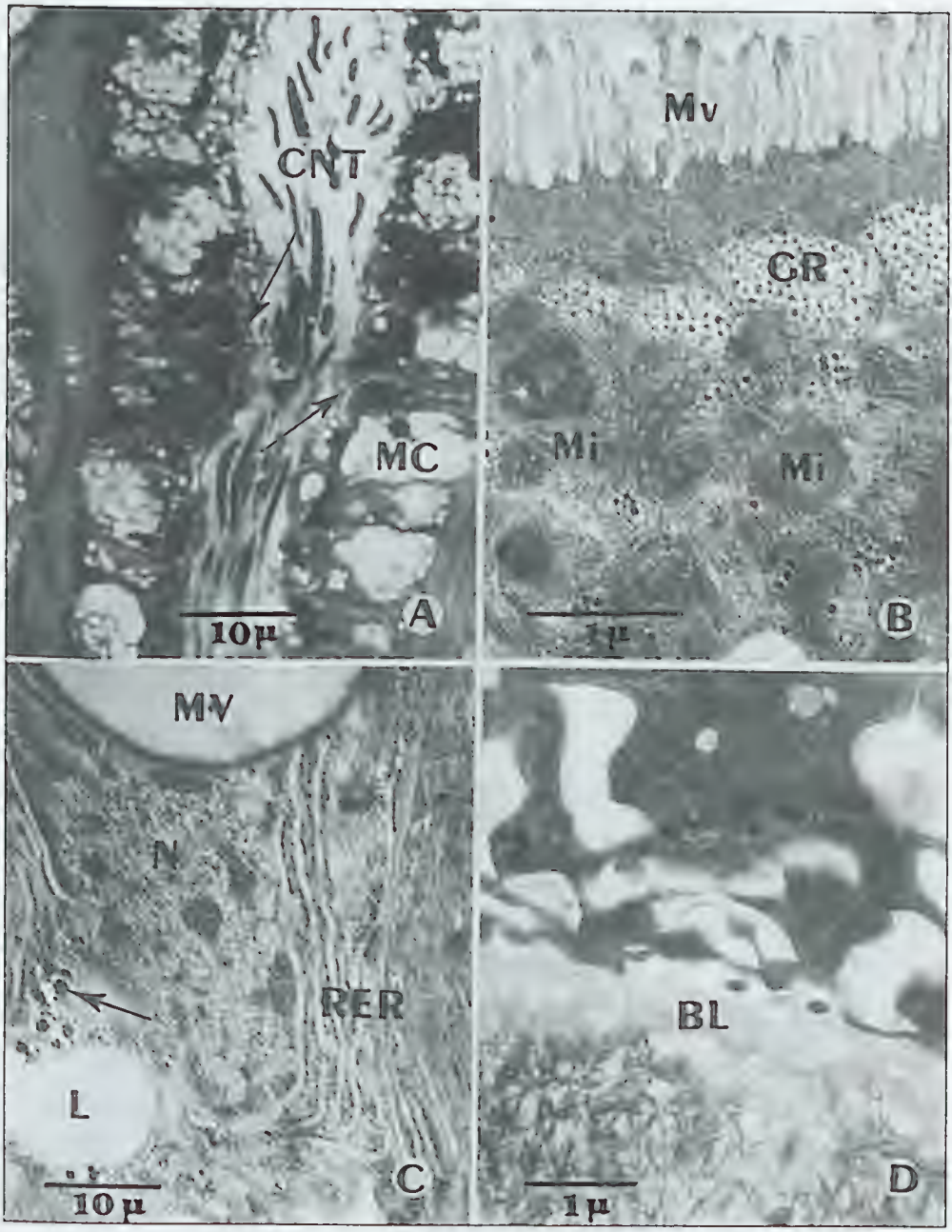

Figure 1. Light (A) and electron (B-F) micrographs of esophagus epithelia in control snails. **A.** Low magnification showing storage cell (arrows) and mucus cell (MC) located on connective tissue (CNT). **B.** Apex of storage cell bearing microvilli (Mv). Beneath the border of microvilli, mitochondria (Mi) and glycogen rosettes (GR) are visible. **C.** Mucus cell showing nucleus (N), lipid droplet (L) and mucus vacuole (MV), rough endoplasmic reticulum (RER) and glycogen rosettes (arrow). **D.** Basal part of epithelial cells with thin and smooth basal lamina (BL).

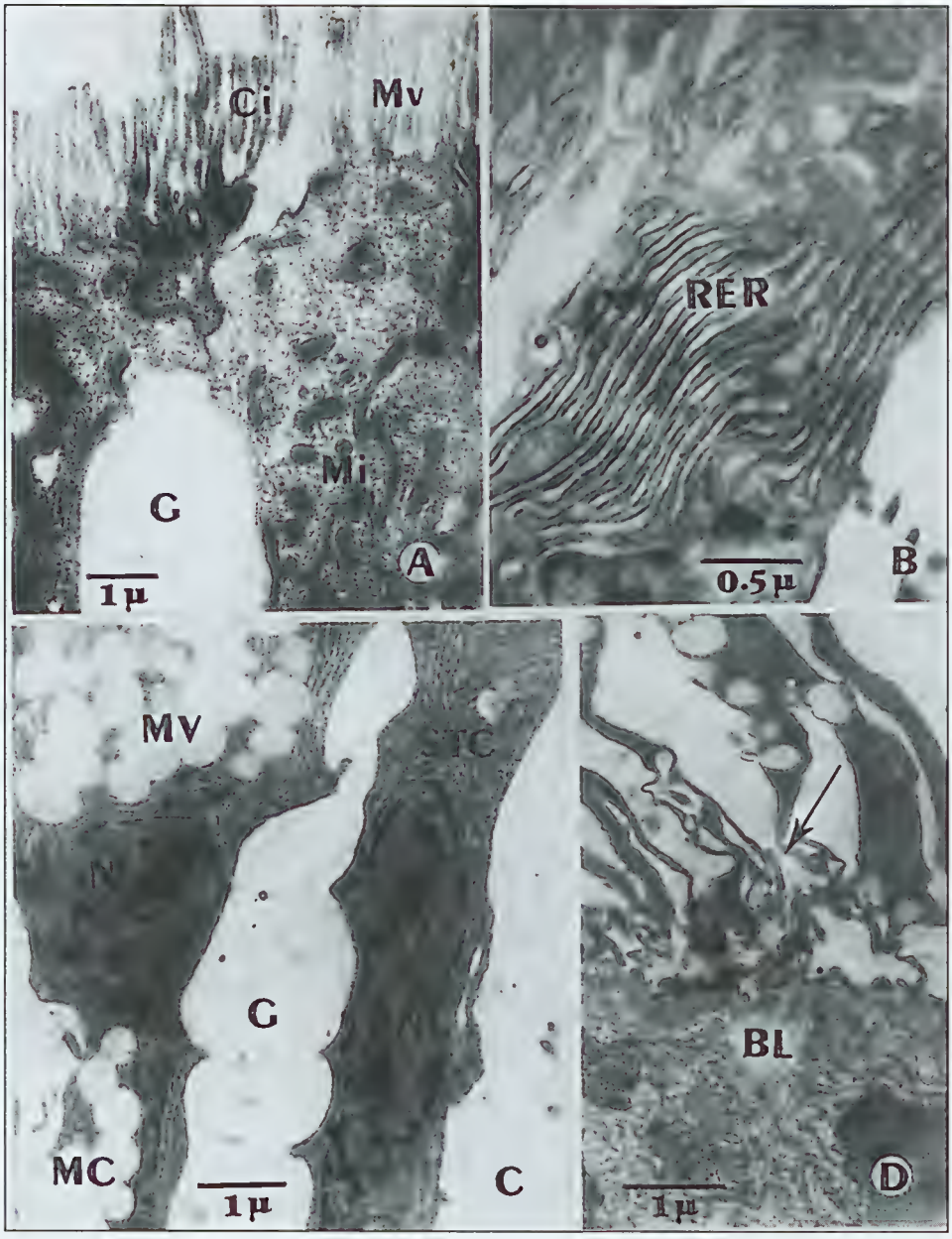

Figure 2. Electron micrographs of esophagus epithelia in snails exposed to niclosamide and *B. actiophylla.* **A.** Storage (STC) in *B. actinophylla* intoxicated snails. Storage cell contains numerous mitochondria (Mi). Note the presence of a large gap (G) between cells. Mv = microvilli, Ci = cilia. . **B.** Storage cell showing degranulation and slight dilation of rough endoplasmic reticulum (RER). **C.** High magnification showing nuclei (N) of mucus cell (MC) and storage cell (STC) with large patches of heterochromatin. Fusion of small vesicles to form large mucus vacuoles (MV) in mucus cell is observed. G = gap. **D.** Basal lamina (BL) showing thickening and increase in infoldings (arrow).

The most striking cytological alterations occur in the mucus cells. There is an increased production of mucus and an intensified fusion of mucus vacuoles (Fig.2C). In the snails intoxicated with either molluscicides, the columnar storage and mucus cells contained nuclei of irregular shape with patches of heterochromatin (Fig. 2C). Large gaps had formed between two adjacent columnar cells (Figs. 2A,2C). In addition, the number of infoldings of the basal lamina had increased (Fig.2D).

Intestine

In control snails, the intestinal epithelium is made up of three cell types, columnar storage cells, secretory cells and mucus cells (Figs. 3A, 3B). Secretory cells predominate.

The storage cells bear both microvilli and cilia and contain numerous mitochondria, regularly-arranged RER, Golgi apparatus and glycogen rosettes (Fig. 3C). Nuclei with nucleoli and patches of heterochromatin are located in the center or subcenter of the cells (Fig.3B). The secretory cells, the most numerous cell type, are characterized by the presence of numerous secretory granules, mitochondria, stacks of RER and well-developed Golgi apparatus (Figs.3B, 3D). The mucus cells are rarely observed and those present contain large mucus vacuoles (Fig3A). The basal part of the epithelium contains small infoldings and the basal lamina is thin (Fig.3E).

The cytological alterations of the intestinal epithelium in niclosamide and *B. actinophylla* intoxicated snails are similar (Fig.4). There is a decrease in number of secretory cells and an increase in number of mucus cells with large mucus vacuoles. Fusion of small vacuoles into large mucus vacuoles was observed (Fig.4A).

The columnar storage cells have undergone some striking changes. There is an increase in number of lysosomes (Fig.4B). Mitochondria remain numerous but show some swelling of cristae (Fig.4B). There is degranulation and dilation of RER (Fig.4C). Membrane whorls of RER could be observed (Fig.4D). Glycogen rosettes are not present. The cell membranes are destroyed in some areas and gaps occur between cells (Fig.4D). The alterations in the nucleus include lightening of karyoplasm and reduction of heterochromatin (Fig.4D). The basal lamina of epithelial cells has become thickened with the increase in infoldings (Fig.4E).

Digestive gland

Control snails

The digestive gland of *I. exustus* is arranged in tubules that are bound together by connective tissue. Four main types of cell can be distinguished in the digestive gland, digestive cell, secretory cell, excretory cell and thin cell (Fig.5A).

Digestive cell Digestive cells which form the major component in the gland, are columnar in shape, vary greatly in length within the same tubule and usually possess microvilli (Fig.5B). The conspicuous vacuoles vary in size (Fig.5B). A few mitochondria and scattered RER are present in the cytoplasm. Lipid and glycogen rosettes can be found. The nuclei of these cells are located in the basal region (Fig.5B).

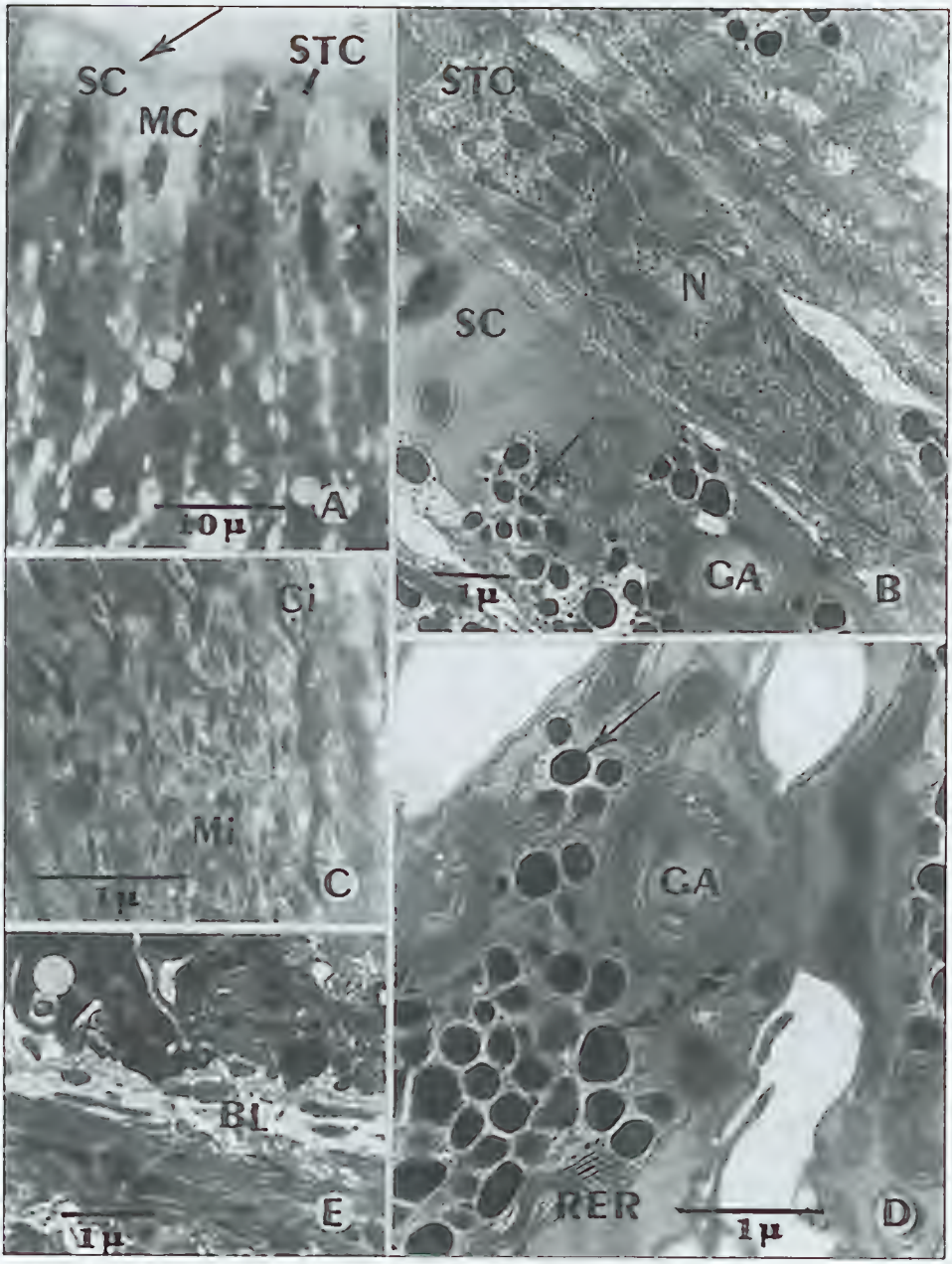

Figure 3. Light (A) and electron (B-F) micrographs of intestinal epithelia in control snails. **A.** Lining epithelium of intestine, showing storage cell (STC), secretory cell (SC) and mucus cell (MC) with brush border (arrow) composed of cilia and microvilli. **B.** Low magnification of storage cell (STC) with long nucleus (N) and secretory cell (SC) with secretory vesicles (arrow) and Golgi apparatus (GA). **C.** Apex of storage cell (STC) bearing cilia (Ci). Beneath the apical surface of the cell, mitochondria (Mi), are visible. **D.** Secretory cell showing Golgi apparatus (GA), and secretory vesicles with electron-dense material (arrows). RER = rough endoplasmic reticulum. **E.** Basal part of epithelial cells with thin and smooth basal lamina (BL).

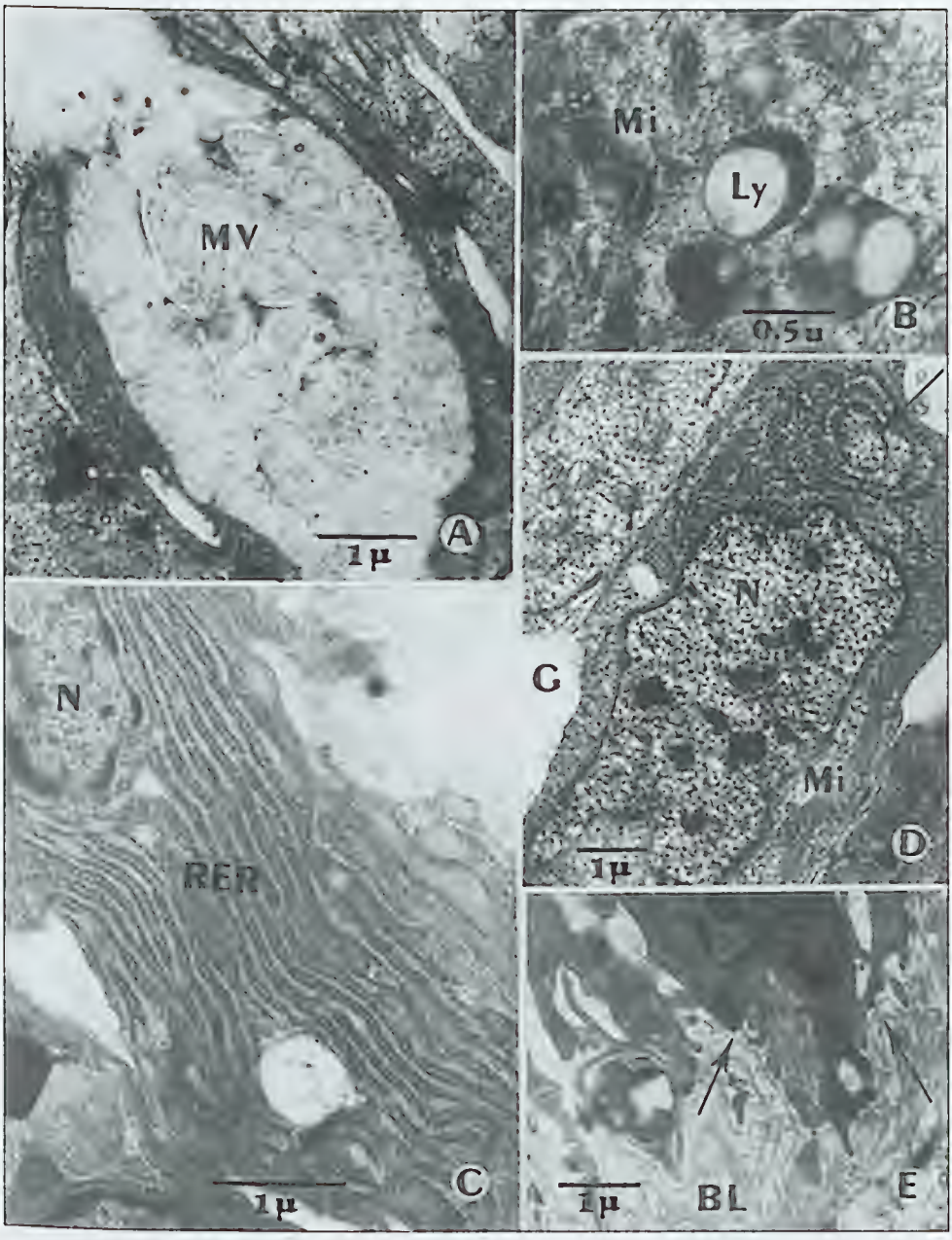

Figure 4. Electron micrographs of intestinal epithelia in niclosamide and *B. actinophylla* intoxicated snails. **A.** Mucus cell showing mucus vacuole (MV) with mucus which is being secreted into the lumen. **B.** Storage cell showing lysosomes (Ly) and mitochondria with swelling cristae (Mi). **D.** Storage cell showing membrane whorls of rough endoplasmic reticulum (RER) in cytoplasm and a decrease of heterochromatin in the nucleus (N). G = gap. Mi = mitochondria. **C.** Storage cell showing dilation and degranulation of rough endoplasmic reticulum (RER). N = nucleus. E. Basal lamina (BL) showing numerous infoldings (arrows).

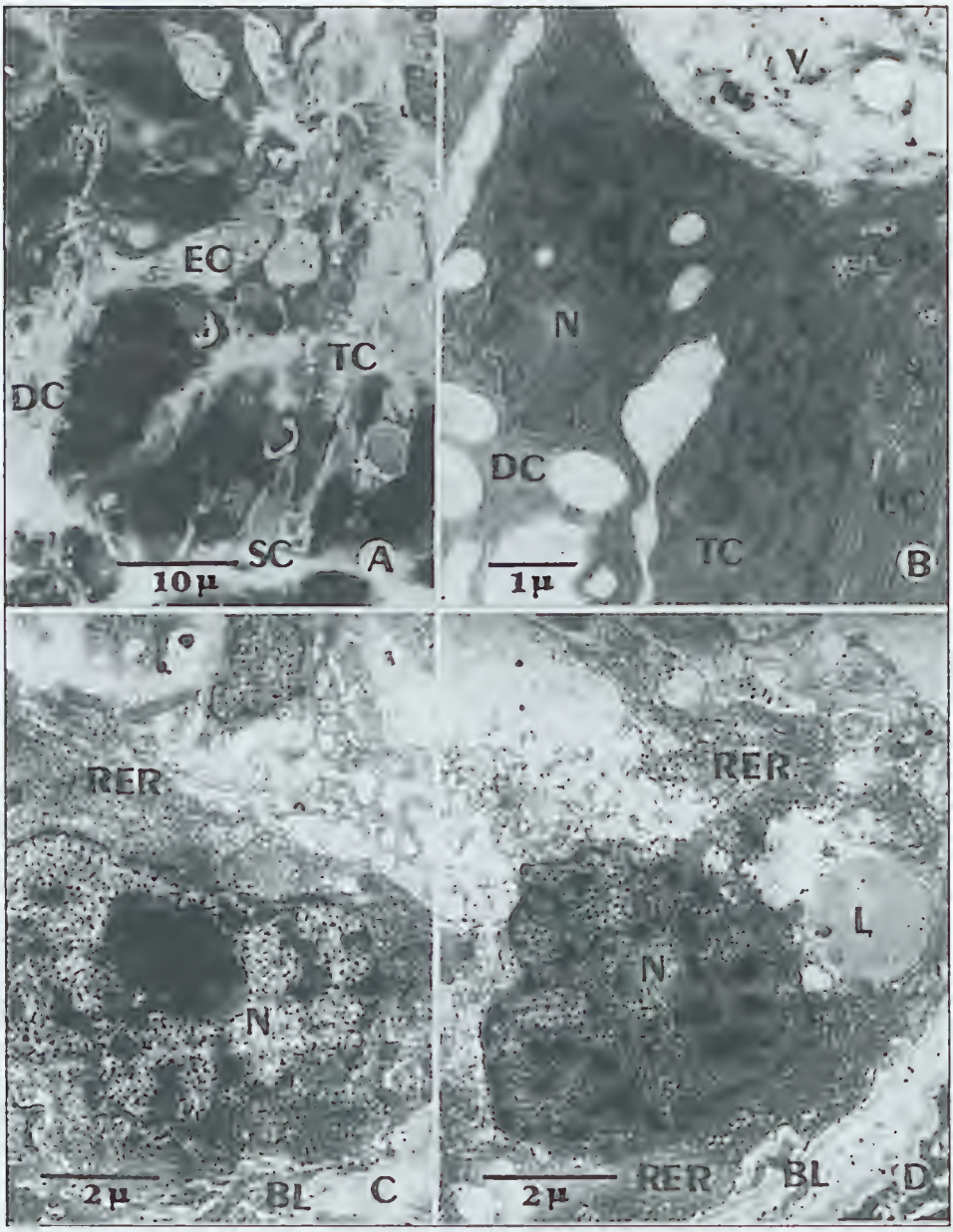

Figure 5. Light (A) and electron micrographs (B-E) of digestive gland epithelia in control snails. **A.** Epithelium of digestive gland tubule showing digestive cells (DC), excretory cells (EC), secretory cells (SC) and thin cells (TC). **B.** Various cell types of digestive gland, digestive cell (DC) with large vacuole (V) containing membranous material, thin cell (TC) with glycogen rosettes (GR), excretory cell (EC) with stacks of rough endoplasmic reticulum (arrow). N=nucleus. **C.** Secretory cell with abundant rough endoplasmic reticulum (RER). BL = basal lamina, N = nucleus. **D.** Excretory cell with abundant rough endoplasmic reticulum (RER). N = nucleus, L = lipid droplet, BL = basal lamina.

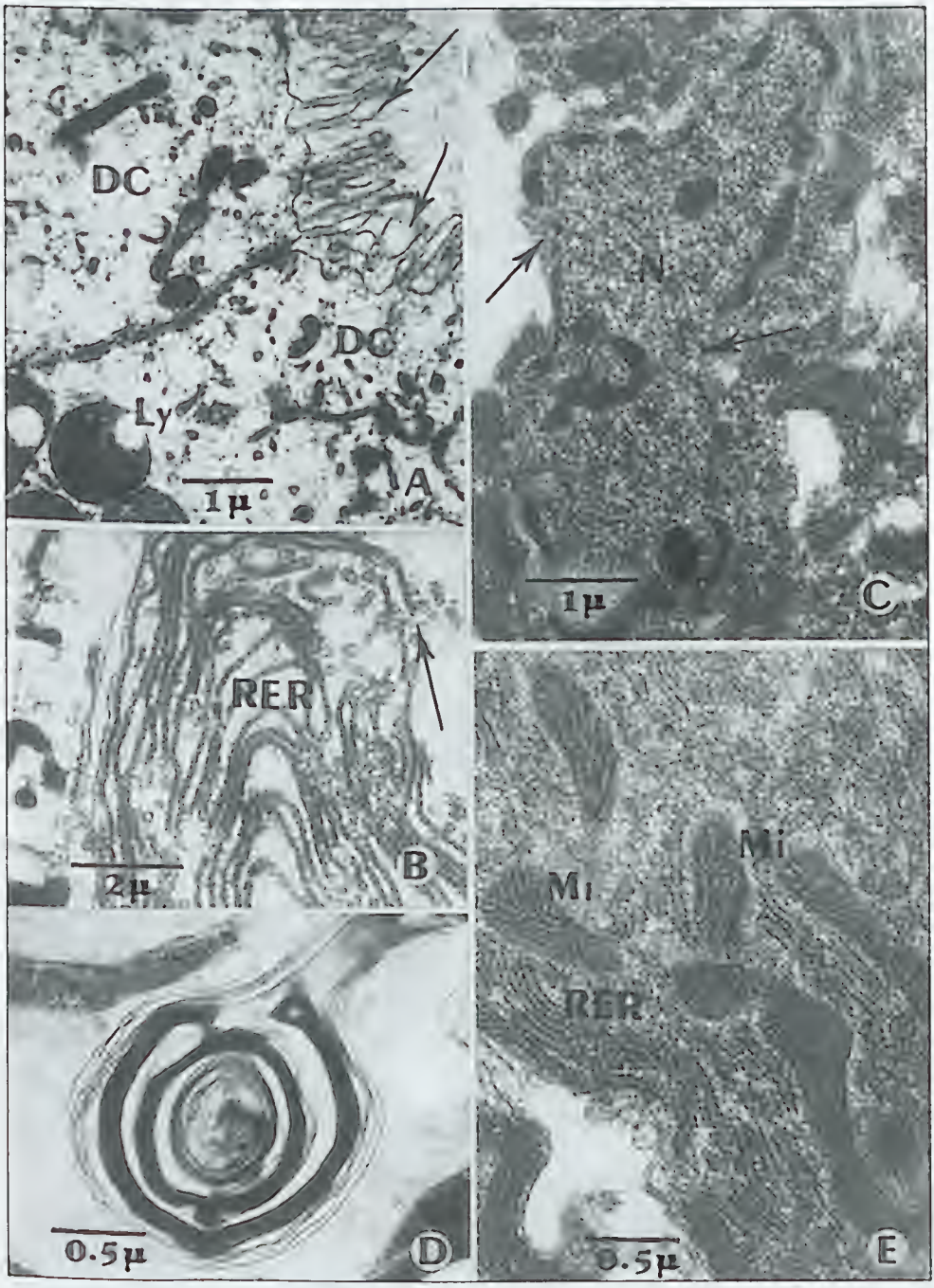

Figure 6. Electron micrographs of digestive gland epithelia in niclosamide intoxicated snails. **A.** Apical part of cells, showing surface blebs and dilation of microvilli (arrows) of digestive cells (DC). Ly = lysosome. **B.** Digestive cell showing fragmentation (arrow) of rough endoplasmic reticulum (RER). **C.** Digestive cell showing disruption of nuclear membrane (arrows). N = nucleus. **D.** Secretory cell showing myelin-like figure. **E.** Secretory cell showing irregular arrangement and swelling of cristae in mitochondria (Mi) and degranulation and fragmentation of rough endoplasmic reticulum (RER).

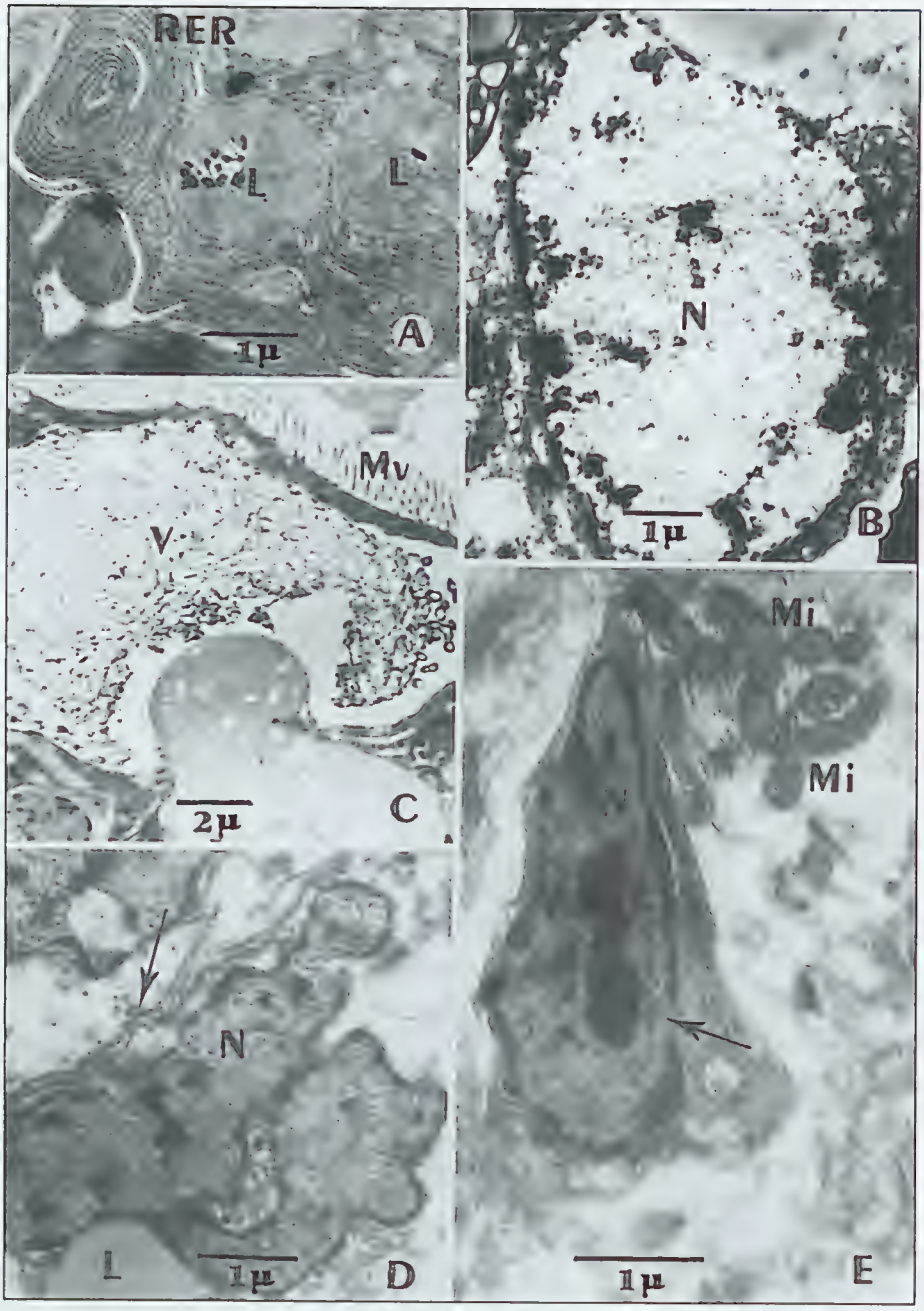

Figure 7. Electron micrographs of digestive gland epithelia in *B. actinophylla* intoxicated snails. **A.** Excretory cell showing membrane whorls of rough endoplasmic reticulum (RER) around lipid droplets (L). **B.** Excretory cell showing karyolysis of nucleus (N). **C.** Excretory cell showing large vacuole containing electron-dense material (V). Mv = microvilli. **D.** Secretory cell showing irregular nucleus (N) and fragmentation of rough endoplasmic reticulum (arrow). L = lipid droplet. **E.** Thin cell showing pycnotic nucleus (N) with disruption of nuclear membrane (arrow) and swelling of cristae and mitochondria (Mi).

Secretory cell Secretory cells usually occur singly in the corner of the tubules. They are pyramidal or conical in shape with broad bases, occasionally abutting into the hemolymph space (Fig.5C). There is a large central or basal nucleus with scattered patches of heterochromatin (Fig.5C).

Excretory cell Excretory cells are larger than digestive cells. The apical surface of this cell type has a dense brush border of microvilli. In the cytoplasm, a small Golgi apparatus, a small number of lipid droplets, mitochondria and extensive RER can be found (Fig.5D). The nucleus is usually positioned in the basal region (Fig.5D).

Thin cell Thin cells are usually situated between digestive cells and secretory cells. They have a border of microvilli. Several mitochondria, free ribosomes and glycogen rosettes are found in the apical cytoplasm (Fig.5B). The nucleus is situated in the center of the cell (Fig.5B).

Molluscicide intoxicated snails

Niclosamide and the crude - aqueous extract of *B. actinophylla* caused alterations in the general outline of cells and in their apical and basal surfaces. The cells of the digestive gland have become irregularly shaped and gaps developed between the epithelial cells. Cytoplasmic protrusions (small surface blebs) were formed. There was slight elongation of microvilli. Glycogen rosettes were no longer visible in the cytoplasm (Fig.6A).

Digestive cell The most striking cytological alterations in the digestive cells of snails exposed to molluscicides were fragmentation of membrane whorls of RER (Fig.6B), fusion of small vacuoles and a decrease in glycogen. In the nucleus, the nuclear membrane was partially destroyed and there was a reduction in heterochromatin (Fig.6C).

Secretory cell Cytological alterations in secretory cells were similar to those in digestive cells. There was a formation of myelin-like figures (Fig.6D). Swelling of mitochondria and cristae was observed (Fig.6E). The nucleus became irregular in shape with reduction in heterochromatin (Fig.7D).

Excretory cell Cytological alterations in excretory cells are quite similar to those in digestive and secretory cells. There are dilation and fragmentation of RER and swelling of mitochondria and cristae. In addition, there was a formation of membrane whorls of RER around the lipid droplets (Fig.7A). Alterations in the nucleus were disruption of nuclear membrane and karyolysis (Fig.7B). In the most severe cases, the cytoplasm was replaced by a large vacuole (Fig.7C) or the whole cell content was extruded into the lumen.

Thin cell Cytological alterations in thin cells were similar to those in secretory and excretory cells with a dilation of RER, swelling of mitochondria and cristae, pycnosis of nucleus and disruption of nuclear membrane (Fig.7E).

Discussion

The general cytological alterations that occurred in the epithelium of the digestive tract of *I. exustus* exposed to niclosamide and *B. actinophylla* were the formation of blebs and the increased fusion of vacuoles, an increase in infoldings of basal lamina, degranulation and dilation of RER, a formation of myelin-like figures, and an increase in mucus production. Most of the reactions were more

severe in snails intoxicated with *B. actinophylla* than those exposed to niclosamide.

The formation of blebs and the increased fusion of vacuoles as results of toxicants or molluscicides had been described in some molluscs. The study of Triebskorn & Künast (1990) on the digestive cells of digestive gland of *D. reticulatum* showed that after intoxication, the intensified fusion between small and large vacuoles resulted in an increase in the number of large vacuoles. In the present study, the increase of large vacuoles and increased fusion of small and large vacuoles occurred in both niclosamide and *B. actinophylla* intoxicated snails. These might result from the interaction of the lipophilic molluscicide with membranes which might induce changes in composition, fluidity and finally stability of the membranes (Triebskorn & Künast, 1990).

Another histological alteration that occurred in the epithelial lining of esophagus and intestine in snails exposed to the molluscicides was the increase in infoldings of basal lamina. Kruatrachue *et al.* (in press) also found the thickening of basement membrane in *Filopaludina (Siamopaludina) martensi martensi* (Frauenfeldt) exposed to lead at the LC80 concentration for 96 hours. This alteration also occurred in *D. reticulatum* exposed to carbamate molluscicide (Triebskorn & Künast, 1990). Triebskorn & Künast (1990) suggested that thickening of the basement membrane might prevent further penetration of the toxin from either the lumen of the digestive tract or from the hemolymph space.

Degranulation and dilation of RER and the formation of myelin-like figures were observed in storage cells of esophagus and intestine, and in digestive and excretory cells of digestive glands of intoxicated *I. exustus*. Reactions of the RER have often been seen in both vertebrates (Sivarajah *et al.*, 1978; Klaunig *et al.*, 1979) and invertebrates, such as mussels (Nott and Moore, 1987) and *D. reticulatum* exposed to molluscicides (Triebskorn 1989; 1991, Triebskorn & Künast, 1990). Several reactions in subcellular organelles such as degranulation of endoplasmic reticulum and the formation of membrane whorls of fingerprint-like structures have been considered as specific stress symptoms or lesions (Rez, 1986). They are general changes of the cell in response to toxicants (Rez, 1986). Most of these reactions are attributed to membrane destabilization and increased membrane permeability to ions under the influence of toxicants (Sparks, 1972).

Increases of mucus in mucus cells and also of mucus cell number were observed in the esophagus and intestine of intoxicated *I. exustus*. The increase of mucus in the lumen of the digestive tract and production of mucus vacuoles due to increased activity of the secretory system (endoplasmic reticulum and Golgi apparatus) are immediate responses to the ingestion of lethal doses of molluscicides. The mucus might serve to dilute toxin and protect the cells of the digestive tract from damage by molluscicides. These reactions of exudate mucus had been observed in *D. reticulatum* (Triebskorn & Künast, 1990). It has been proposed that mucus cells have a protective and detoxifying function (Zylstra, 1972 a; 1972b; 1972c; Moya & Rallo, 1975). Moreover, snails are capable both of increasing the quantity, and of varying the quality, of the chemical composition of mucus (Triebskorn & Ebert, 1989). The exudation of acidic mucus can be regarded as a kind of incidental detoxification, because the toxin is less stable under acidic conditions. Nevertheless, the reason for the alteration in the

chemical composition of the mucus is not known (Triebskorn & Künast, 1990). We agree with the conclusion of Triebskorn & Künast (1990) that the induction of mucus secretion could finally lead to the desiccation and death of snails. The intensified exudation of mucus can kill snails and specific molluscicides do not only enhance secretion of mucus but also damage the ultrastructure of cells. Airey *et al.* (1989) regarded the mucus cells as one of the target for specific molluscicidal interference.

An increased use of energy on resources to initiate protective or detoxification processes might lead to a quick reduction of lipid and glycogen in the storage cells. Triebskorn & Künast (1990) also described the reduction of glycogen and lipid in storage cells of *D. reticulatum* intoxicated by carbamate. Dillaman (1980) reported the disappearance of glycogen rosettes in the ureter cells of kidney in the freshwater snail, *Helisoma anceps* Menke exposed to low concentrations of cadmium. We also observed a reduction in glycogen content in the storage cells of esophagus and digestive cells of the digestive gland of *I. exustus* exposed to niclosamide and *B. actinophylla*.

The main cell types of digestive gland are digestive cell, secretory cell, thin cell and excretory cell. Similar cells have been described for *Agriolimax reticulatus* (Muller) (Walker, 1970). The secretory cells serve secretory functions of storage and detoxification and have a characteristic conical outer shape. The excretory cells are characterized by diversity of vacuoles with electron-dense material which is excreted into the lumen of the gland. The digestive cells digest the food by pinocytosis (Bode *et al.*, 1996). In the snails *I. exustus* intoxicated with molluscicides, the digestive gland was highly affected. Some tubules were observed to be in the process of autolysis. The increased amount of lysosomal activity and extensive autolysis were also reported in the hepatopancreas of fiddler crab, *Uca minax* exposed to naphthalene (Robinson & Dillaman, 1985). In pathological conditions, autolysis of cells is commonly the result of the release of digestive enzymes into the cytoplasm after destruction of the lysosomal membranes.

Similar cytological alterations were observed in different cell types of digestive gland (digestive, excretory, secretory and thin cells) of intoxicated *I. exustus*. There was dilation and fragmentation of RER, swelling of mitochondria and cristae, pycnosis and karyolysis of nucleus and disruption of nuclear membrane. These ultrastructural changes are usually observed in invertebrates exposed to sublethal concentrations of pollutants (Papathanassiou & King, 1983; Robinson & Dillaman, 1985; Marigómez *et al.*, 1990). Dilation of rough endoplasmic reticulum and nuclear pycnosis were observed in the kidney epithelial cells of *Littorina littorea* (Linnaeus) treated with sublethal concentration of cadmium (Marigómez *et al.*, 1990) and in the hepatopancreas of *U. minax* exposed to naphthalene (Robinson & Dillaman, 1985). Although the rough endoplasmic reticulum was not destroyed, its structure was altered to the extent that its synthetic function could have been impaired (Robinson & Dillaman, 1985).Nuclear pycnosis as observed in the digestive gland cells of *I. exustus* and in the kidney epithelial cells of *L. littorea* usually indicates a serious injury to metabolic or regulatory processes.

The reactions of mitochondria, swelling and reduction of cristae and disruption of mitochondrial membrane are interpreted as a sublethally induced stress response to molluscicides or pollutants. Papathanassiou & King ((1983) reported irregular mitochondria with reduction of cristae in the gill lamellae of common shrimp, *Palaemon serratus* exposed to cadmium. Disruption of mitochondrial membrane was reported in the renal epithelium of *L. littorea* treated with cadmium (Marigómez *et al.*, 1990), in the absorptive cells of hepatopancreas in *U. minax* exposed to naphthalene, and in the gill lamellae of *P. serratus* exposed to cadmium. These alterations of mitochondria could reflect a response to factors inhibiting the passage of substrates for oxidation into the mitochondria leading to ATP-deficiency and subsequently metabolic activity (Papathanassiou & King, 1983; Robinson & Dillaman, 1985). Triebskorn & Künast (1990) assumed that the swelling of mitochondria and reduction of cristae could be induced in various ways by exogenous or endogenous stress. Even if the symptoms are similar, the causes of the response might be totally different.

References

Adewunmi, C.D. & Ogbe, M.G. 1986. The histopathology of *Tetrapleura tetraptera* extract on some freshwater snails. *Filoterapia* **57:** 371-374.

Airey, W.J., Henderson, I.F., Picket, J.A., Scott, G.C., Stephenson, J.W., & Woodcock, C.M. 1989. Novel chemical approaches to mollusc control. *Proceedings of the British Crop Protection Council* **41:** 301-308.

Bode, A.U.D., Adewunmi, C.O., Dorfler, G. & Becker, W. 1996. The effects of extracts from *Tetrapleura tetraptera* (Taub.) and Bayluscide on cells and tissue structures of *Biomphalaria glabrata* (Say). *Journal of Ethnopharmacology* **50:** 103-113.

Bourne, N.B., Jane, G.W. & Bowen, I.D. 1991. Endocytosis in the crop of the slug *Deroceras reticulatum* (Müller) and the effects of the ingested molluscicides, metaldehyde and methiocarb. *Journal of Molluscan Studies* **57:** 71-80.

Dillaman, R.M. 1980. Toxicity of cadmium to *Helisoma anceps* and its effect on kidney ultrastructure. *Journal of Invertebrate Pathology* **36:** 223-234.

Klaunig, J.E., Lipsky, M.M., Trump, B.F. & Hinton, E. 1979. Biochemical and ultrastructural changes in teleost liver following subacute exposure to PCB. *Journal of Environmental Toxicology* **2:** 953-963.

Kruatrachue, M., Upatham, E.S., Sretarugsa, P., Chitramvong, Y., Singhakaew,S. & Parkpoomkamol, K. 1997. The effects of lead on structure of the digestive system of *Filopaludina (Siamopaludina) martensi martensi* (Gastropoda : Prosobranchia). *Journal of Medical and Applied Malacology* (in press).

Marigómez, J.A., Cajaraville, M.P., Angulo, E. & Moya, J. 1990. Ultrastructural alterations in the renal epithelium of cadmium-treated *Littorina littorea* (L.). *Archives of Environmental Contamination and Toxicology* **19:** 863-871.

Moya, J. & Rallo, A.M. 1975. Intercisternal polycylinders : a cytoplasmic structure in cells of the terrestrial slug *Arion empiricorum* (Férussac) Pulmonata, Stylommatophora. *Cell Tissues Research* **159:** 423-433.

Nott, J.A. & Moore, M.N. 1987. Effects of polycyclic aromatic hydrocarbons on molluscan lysosomes and endoplasmic reticulum. *Histochemical Journal* **19:** 357-368.

Papathanassiou, E. & King, P.E. 1983. Ultrastructural studies on the gills of *Palaemon serratus* (Pennant) in relation to cadmium accumulation. *Aquatic Toxicology* **3:** 273-284.

Rez, G. 1986. Electron microscopic approaches to environment toxicity. *Acta Biologica Hungarica* **37(1):** 31-45.

Robinson, A.G. & Dillaman, R.M. 1985. The effects of naphthalene on the ultrastructure of the hepatopancreas of the fiddler crab, *Uca minax*. *Journal of Invertebrate Pathology* **45:** 311-323.

Sivarajah, K., Franklin, C.S. & Williams, W.P. 1978. Some histopathological effects of Arochlor 1254 on the liver and gonads of rainbow trout *Salmo gairdneri* and carp, *Cyprinus carpio*. *Journal of Fish Biology* **13:** 411-414.

Sparks, A.K. 1972. Invertebrate Pathology, Non-communicable Diseases. Academic Press, New York.

Triebskorn, R., 1989. Ultrastructural changes in the digestive system of *Deroceras reticulatum* (Müller) induced by a carbamate molluscicide and by metaldehyde. *Malacologia* **31(1):** 141-156.

Triebskorn, R. 1991. Cytological changes in the digestive system of slugs induced by molluscicides. *Journal of Medical and Applied Malacology* **3:** 113-123.

Triebskorn, R. & Ebert, D. 1989. The importance of mucus production in slugs reaction to molluscicides and the impact of molluscicides on the mucus producing system. *Proceedings of the British Crop Protection Council* **41:** 373-379.

Triebskorn, R. & Künast, C. 1990. Ultrastructural changes in the digestive system of *Deroceras reticulatum* (Mollusca : Gastropoda) induced by lethal and sublethal concentrations of the carbamate molluscicide cloethocarb. *Malacologia* **32(1):** 89-106.

Upatham, E.S., Wangsomnuk, P., Kruatrachue, M., Chitramvong, Y.P. & Reutrakul, V. 1998. Acute toxicity of a plant molluscicide, *Brassaia actinophylla* on *Indoplanorbis exustus* and non-target organisms. *Molluscan Research* (in press).

Walker, G. 1970. The cytology, histology, and ultrastructure of the cell types found in the digestive gland of the slug, *Agriolimax reticulatus* (Müller). *Protoplasma* **71:** 91-109.

Zylstra, U. 1972a. Histochemistry and ultrastructure of the epidermis and the subepidermal gland cells of the freshwater snails *Lymnaea stagnalis* and *Biomphalaria pfeifferi*. *Zeitschrift für Zellforschung und Mikroskopische Anatomie* **130:** 93-134.

Zylstra, U. 1972b. Distribution and ultrastructure of the epidermal sensory cells in the freshwater snails *Lymnaea stagnalis* and *Biomphalaria pfeifferi*. *Netherland Journal of Zoology* **22:** 283-298.

Zylstra, U. 1972c. Uptake of particular matter by the epidermis of the freshwater snails *Lymnaea stagnalis*. *Netherland Journal of Zoology* **22:** 299-306.

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Population genetic structure of the muricid gastropod *Lepsiella vinosa* in Gulf St Vincent, South Australia

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Abstract

Allozyme electrophoresis was used to examine the population genetic structure of the marine gastropod *Lepsiella vinosa*, which produces benthic egg capsules with crawling juveniles. Samples of *L. vinosa*, taken from five locations along the coast of Gulf St Vincent, South Australia, including replicate samples within three of the locations, were examined for allozyme variation at four polymorphic loci (*Acon-1, Got, Gpi* and *Lap*). Genotypic frequencies were consistent with expectations under conditions of Hardy-Weinberg equilibrium. Genetic divergence between samples separated by only 500 m was small, in contrast to the great divergence found between samples separated by more than 10 km. This degree of genetic divergence ($F_{ST} = 0.200 \pm 0.073$; Nei's D mean = 0.071) indicated low gene flow ($N_em = 1.08$ immigrants per generation) over distances $\geq$ 10 km. The data are consistent with a 'discrete subpopulation model'.

Key words : population, genetic structure, *Lepsiella vinosa*, South Australia.

Introduction

The dispersal ability of sedentary benthic marine invertebrates is largely predicted by their mode of larval development. Species with extensive dispersal, such as those with long planktonic larval stages, tend to have a broad distribution and little genetic differentiation among populations over large distances (Scheltema 1971, 1986; Hedgecock 1986; Janson 1987; Ovenden *et al.* 1992; Parsons 1996). In contrast, species with limited dispersal, such as those lacking a planktonic larval phase, tend to have a restricted distribution and high levels of genetic differentiation between populations (Snyder & Gooch 1973; Crisp 1978; Burton 1983; Johnson & Black 1984; Grant & Utter 1988). In these latter species, allele frequencies can be significantly different in populations separated by only a few hundred metres (Janson & Ward 1984; Grant & Utter 1988; Carvalho & Piertney 1997).

There are, however, several notable exceptions. For example, some brooding invertebrates that lack a planktonic larval stage are more widespread than related species that have a planktonic dispersive phase (Highsmith 1985; Johannesson 1988; Martel & Chia 1991). This implies that brooding invertebrates have alternative mechanisms for dispersal. One possible such mechanism is dispersal by attachment to floating objects, *i.e.* rafting (O'Foighil 1989; Martel & Chia 1991). Indeed, several authors have suggested that rafting of sedentary benthic invertebrates with direct development may be a more powerful means of long distance dispersal than is larval diffusion (Dell 1972; Jackson 1986; Johannesson 1988). Another potential dispersal mechanism is floating. Although dispersal by floating is generally limited to a local scale and is restricted to smaller invertebrates, it does increase the probability of rafting and thus long distance dispersal (Highsmith 1985).

A second notable exception to the relationship between larval development and geographic distribution is the presence of population subdivision in species with planktonic larvae (Burton 1983; Hedgecock 1986; O'Foighil 1989; Parsons 1996). This subdivision may be driven by selective forces, which vary between age classes and from habitat to habitat (e.g. Koehn *et al.* 1976), or it may be attributable to a variety of biological or physical processes that restrict dispersal (reviewed by Hedgecock 1986).

Lepsiella vinosa (Lamarck 1882) is a dioecious, muricid gastropod found abundantly in the intertidal region along the coastline of southern Australia from NSW to Albany, WA (Macpherson & Gabriel 1962; Wilson & Gillet 1974). Unlike most marine gastropods, this species lays gelatinous egg capsules which hatch to liberate crawling juveniles (Synnot 1980; Smith *et al.* 1989). This mode of development coupled with the relatively sedentary behaviour of the adults limits their potential for dispersal. The wide geographical range of *L. vinosa* contrasts with its apparent limited dispersal ability, making it a noteworthy candidate for examination. The main objective of the present study was to examine the genetic differentiation of this species and thus infer its dispersal ability.

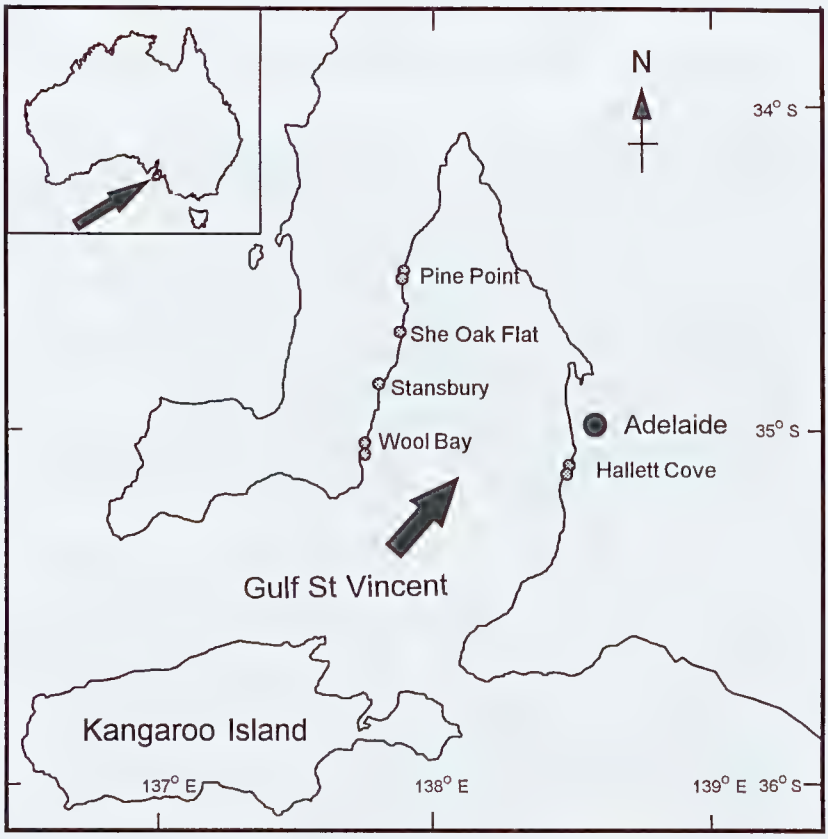

Figure 1. Map showing collection sites in Gulf St Vincent , South Australia

Materials and Methods

Collection of samples

Samples of *L. vinosa* were collected from five intertidal locations, 10-80 km apart, along the coast of Gulf St Vincent, during November 1992 and January 1993 (Fig. 1).

At the same time, additional samples were collected at Hallett Cove, Wool Bay and Pine Point from sites less than 500 m from the original collection. These additional samples were used to measure genetic variation within a location (*i.e.* at a spatial scale smaller than the span of the location). At each site, individuals were randomly collected from the smallest area possible, usually from an area less than 3 m^2. Each sample was kept in a separate tank filled with aerated sea water, for a minimum of ten days without food, to eliminate the possibility of spurious electrophoretic patterns due to gut contents.

Allozyme electrophoresis

Materials and methods used for electrophoresis follow the procedures of Richardson *et al.* (1986). The shell was carefully crushed and the hepatopancreas dissected out. The hepatopancreas was homogenised in an equal volume of lysis buffer (0.01% NADP, 0.01% 2-mercaptoethanol, distilled H_2O). Homogenates were centrifuged at 10,000 g for 10 minutes, and the supernatant transferred into separate capillary tubes and stored at -80°C, pending electrophoresis. Interpretations of gels were made with reference to the predicted quaternary structure of the enzyme and band patterns of putative heterozygotes (Richardson *et al.* 1986).

A pilot study was conducted by screening 40 enzyme systems on 40 individuals (5 from each sample) to identify polymorphic loci and to optimise electrophoretic conditions. Four polymorphic loci (*Acon -1, Got, Gpi* and *Lap*) were screened (Table 1).

Table 1. Enzyme Commission (E.C.) numbers and buffer conditions of the polymorphic enzymes screened.

Enzyme name	Locus	E.C. number	Number of alleles	Buffer system (after Richardson *et al.* 1986).
Aconitate hydratase	*Acon - 1*	4.3.1.3	3	0.02M Phosphate pH 7.0
Aspartate aminotransferase	*Got*	2.6.1.1	2	0.05M Tris Maleate pH 7.8
Glucose phosphate isomerase	*Gpi*	5.3.1.9	2	0.02M Phosphate pH 7.0
Leucine aminopeptidase	*Lap*	3.4.11.1	2	0.01M Citrate Phosphate pH 6.4

As well as having mobility controls on every gel, approximately 10% of all individuals, randomly chosen, were retyped at each locus as a check for scoring consistency. Allozyme phenotypes of putative heterozygotes at the four polymorphic loci were consistent with those expected on the basis of the predicted quaternary structure of the enzymes.

Statistical analysis

Allelic frequencies were calculated for each locus for each of the samples using the BIOSYS-1 program (Swofford & Selander 1981). Locus x locus χ^2 homogeneity tests were used to test the assumption that loci were in linkage equilibrium (Hill 1974). The genotype frequency distribution of each polymorphic locus in each sample was tested for goodness-of-fit to Hardy-Weinberg expectations using a χ^2 test (Siegel 1956) with Levene's (1949) correction for small sample sizes.

Multilocus measures of genetic variability calculated within each sample were:

- **a**, mean number of alleles per locus;
- **P**, the proportion of polymorphic loci whose most common allele is not greater than 0.95 in frequency;
- H_o, the mean heterozygosity per locus observed by direct count of individuals;
- H_e, the unbiased estimate of mean heterozygosity per locus expected under Hardy-Weinberg equilibrium.

The methods for calculation of these measures are given in Nei (1978). Heterozygote deficiencies from Hardy-Weinberg expectations were analysed for each sample using the fixation index of Wright (1978).

Pairwise χ^2 tests for heterogeneity of allele frequencies among locations were performed for all loci (Siegel 1956). The sequential Bonferroni test was used to adjust probabilities for these tests (Rice 1989). The overall genetic differentiation between samples was calculated as Nei's (1978) unbiased measure of genetic distance. The results were represented diagrammatically as a dendrogram in which clustering was determined by the unweighted pair-group method algorithm (UPGMA; Sokal & Sneath 1963). The dendrogram is not intended to reflect phylogenetic relationships, but rather to give a visual indication of the genetic diversity between samples.

For each locus, the magnitude of the allelic variation occurring within location (F_{IS}) and between locations (F_{ST}; Wright 1978) was calculated using the DIPLOID program (Weir 1990). An estimate of the variance of both F_{IS} and F_{ST} was obtained by jackknifing loci, as described by Weir & Cockerham (1984), to obtain 95% confidence limits (DIPLOID; Weir 1990). The significance of F_{IS} and F_{ST} values were tested with χ^2 tests, using equations in Waples (1987). Based on the island model of Wright (1978), values of gene flow among locations were estimated from F_{ST} using the equation $N_em = [(1/F_{ST}) - 1] / 4$, where N_e is the effective population size and m is the migration rate. Estimates of the variance of the mean number of immigrants per generation were obtained by jackknifing loci, to obtain 95% confidence limits for Weir & Cockerham's (1984) F_{ST} and then calculating gene flow N_em from these.

Results

Allele frequencies for each locus for each sample are presented in Table 2. Two alleles were observed at *Got*, *Gpi* and *Lap*, and three alleles at *Acon-1*. *Gpi* and *Got* allele frequencies were dominated in all samples by one allele, while *Acon-1* and

Lap were more variable. *Lap*^{b} had the largest difference in frequency between samples, ranging from 0.36 at Hallett Cove 2 to 0.99 at Pine Point 1. There was no fixed difference between samples as they all shared at least one allele at each locus. The She Oak Flat sample possessed an allele, *Acon-1*^{c} (at a frequency of 0.09), which was absent from other samples.

Table 2. Allele frequencies for *L. vinosa* at four polymorphic loci

Locus	allele	Wool Bay 1	Wool Bay 2	Stansbury	She Oak Flat	Pine Point 1	Pine Point 2	Hallett Cove 1	Hallett Cove 2
Acon - 1	c				0.09				
	b	0.54	0.41	0.50	0.27	0.11	0.21	0.07	0.24
	a	0.46	0.59	0.50	0.64	0.89	0.79	0.93	0.76
Got	b	0.01	0.08			0.10	0.05	0.06	0.06
	a	0.99	0.92	1.00	1.00	0.90	0.95	0.94	0.94
Gpi	b	0.03	0.06	0.04	0.26	0.06	0.04		
	a	0.97	0.94	0.96	0.74	0.94	0.96	1.00	1.00
Lap	b	0.71	0.79	0.49	0.42	0.99	0.93	0.40	0.36
	a	0.29	0.21	0.51	0.58	0.01	0.07	0.60	0.64
	N	57	86	34	81	84	79	87	91

Alleles were labelled alphabetically in order of increasing mobility. Multiple loci encoding the same enzyme (isoenzyme) were designated by consecutive numbers, with '1' denoting the slowest migrating isoenzyme.
N = number of individuals typed.

Locus x locus χ^2 homogeneity tests indicated no linkage disequilibrium ($p>0.05$) between any loci within the eight samples. Therefore each of the four polymorphic loci could be treated as independent tests of the relationship between the samples.

Heterozygosity (H_o, H_e) and the proportion of polymorphic loci varied substantially between samples (Table 3). The proportion of polymorphic loci per sample varied between 50 and 100% with an average of 71%. In addition, levels of mean observed heterozygosity (H_o) were also high (H_o mean = 0.210; H_o range: 0.119-0.312).

The observed heterozygosity (H_o) for each sample conformed with Hardy-Weinberg expectations. Only one significant departure from Hardy-Weinberg expectations was detected, a heterozygote deficit in *Acon-1* at Stansbury ($F = 0.529$). The results for heterozygosity were consistent with χ^2 tests of fit to Hardy-Weinberg expectations for individual loci. Again, there was only one significant departure ($\chi^2 = 10.07$, $p<0.001$) from Hardy-Weinberg equilibrium, namely for *Acon-1* at Stansbury. As there was no deviation from Hardy-Weinberg expectations at samples within locations, the respective replicate samples were pooled and the resulting three populations subjected to further goodness-of-fit tests. All three populations at Wool Bay, Pine Point and Hallett Cove conformed to Hardy-Weinberg expectations.

Table 3. Measures of genetic variability at 4 polymorphic loci for all samples

Site	Mean numbers of alleles per locus	Percentage of polymorphic loci*	Direct count	Hardy Weinberg expected**
	a	P	H_o	H_e
Wool Bay 1	2.0 ± 0.0	50	0.215 ± 0.105	0.246 ± 0.124
Wool Bay 2	2.0 ± 0.0	100	0.247 ± 0.070	0.270 ± 0.087
Stanbury	1.8 ± 0.3	50	0.206 ± 0.109	0.275 ± 0.135
She Oak Flat	2.0 ± 0.4	75	0.312 ± 0.109	0.349 ± 0.120
Pine Point 1	2.0 ± 0.0	75	0.119 ± 0.042	0.125 ± 0.042
Pine Point 2	2.0 ± 0.0	75	0.152 ± 0.048	0.158 ± 0.059
Hallett Cove 1	2.0 ± 0.3	75	0.204 ± 0.120	0.183 ± 0.104
Hallett Cove 2	1.8 ± 0.3	75	0.223 ± 0.100	0.235 ± 0.107
Mean	1.9 ± 0.16	71.9	0.210 ± 0.087	0.230 ± 0.097

* A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95
** Unbiased estimate (see Nei, 1978)

Table 4. F-statistics describing within population structuring (F_{IS}), between population structuring (F_{ST}) and gene flow (N_em) among all samples and only samples from the western coastline of Gulf St Vincent.

	All samples		Western coastline samples	
Locus	F_{IS}	F_{ST}	F_{IS}	F_{ST}
Acon -1	0.141***	0.129***	0.159**	0.117***
Got	-0.039ns	0.021**	-0.21ns	0.037***
Gpi	0.096*	0.123**	0.099*	0.099**
Lap	0.017ns	0.287***	0.070ns	0.274***
Over all loci	0.070ns	0.187***	0.100ns	0.163***
Unbiased F_{ST} ± 95%	0.074 ± 0.5	0.2 ± 0.073	0.11 ± 0.044	0.167 ± 0.06
N_em (range)		1.08 (0.66 - 1.72)		1.28 (0.9 - 2.01)

* P<0.05; ** P<0.01; *** P<0.001; ns, not significant

Many of the χ^2 tests for heterogeneity of allele frequencies were significant at the Bonferroni-adjusted level of 0.00045 (0.05/112). These tests indicated that the She Oak Flat location possessed the most divergent allelic array because it had the largest number of significantly heterogeneous χ^2 tests when compared to the other location. In contrast, there was no significant difference in allelic frequencies within Wool Bay and Pine Point. At Hallett Cove, only *Acon-1* was significant at the $P< 0.00045$ level.

The overall pattern of genetic differentiation of samples was calculated as Nei's (1978) unbiased measure of genetic distance (Table 4). Genetic differentiation was smallest between samples from the same location *ie.* Wool Bay, Pine Point and Hallett Cove (*D* mean = 0.006; *D* range 0.004 to 0.008). Any pairwise comparisons between two locations resulted in much higher values of genetic distance. The mean genetic distance for all possible pairwise comparisons between locations was 0.071, with a range of 0.013 to 0.137. This differentiation was an order of magnitude higher than between pairs of samples from the same location. The values of genetic distance are presented in a dendrogram (Figure 2).

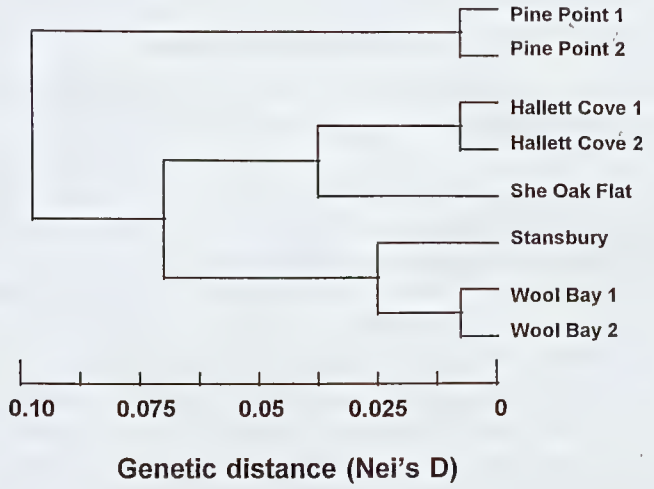

Figure 2. Dendrogram based on Nei's (1978) genetic distance for all samples constructed by UPGMA clustering (Sokal & Sneath 1963)

From the dendrogram, it can be clearly seen that the samples collected within the same location had the highest genetic similarity. Apart from this, and the close geographic proximity and genetic similarity of Stansbury to Wool Bay, clustering did not correspond to that expected from spatial distance alone. For example, according to the dendrogram, She Oak Flat was more similar to Hallett Cove than to its geographically closest neighbour at Pine Point. A pairwise comparison of genetic distance with geographic separation between all combinations of locations also illustrated no clear correlation (Fig. 3). Furthermore, a comparison of allele frequencies, with respect to geographic locations, lacked any apparent trends such as clines, with the fluctuations appearing to be chaotic.

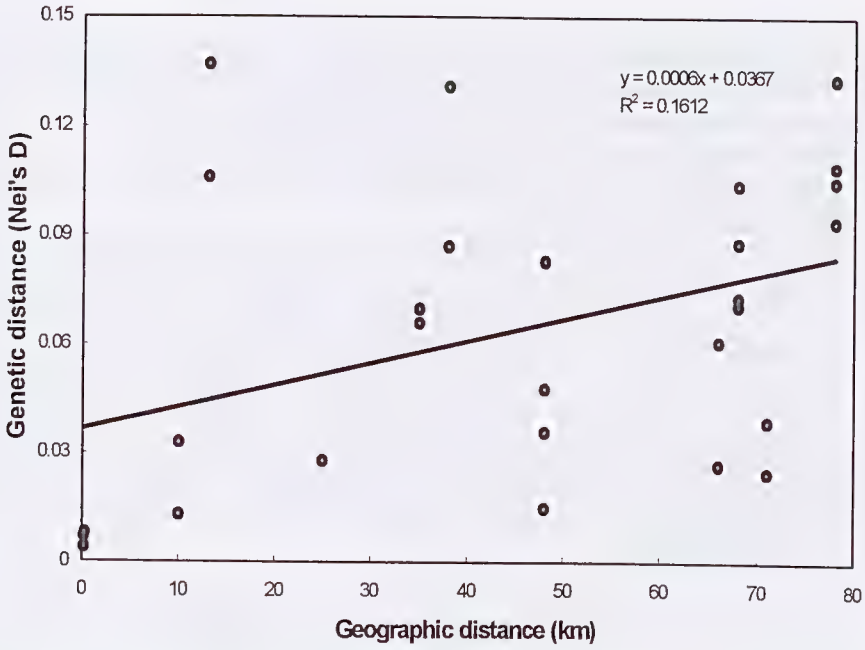

Figure 3. Genetic distance (Nei's *D*) as a function of geographic distance (km; straight line) between pairwise comparison of samples.

Two F_{IS} values for individual loci (*Acon-1* and *Gpi*) were significant, indicating possible within-location substructuring (Table 4). However, the F_{IS} value for *Gpi* was only marginally significant ($F_{IS} = 0.096$, $p<0.05$), and the value for *Acon-1* ($F_{IS} = 0.141$, $p<0.001$) was biased due to the large contribution of variation from the Stansbury location. In addition, the mean F_{IS} value over all loci was non-significant ($F_{IS} = 0.07$). This, and the fact that the detailed χ^2 tests of individual loci failed to demonstrate any significant departures from Hardy-Weinberg expectations (except for *Acon-1* at Stansbury), suggested that within-location substructuring, if present, was below the sensitivity of our methods.

Weir & Cockerham's (1984) F_{ST}, which take into account variation in sample sizes, demonstrated significant differences in allele frequencies among locations for all loci (Table 4). Differentiation among all locations, measured by F_{ST}, ranged from 0.021 for *Got* to 0.287 for *Lap*, with an average for all loci of 0.187 ($p<0.001$). When Hallett Cove was excluded from this analysis, leaving only the locations on the western coastline of the gulf, the genetic differentiation amongst locations ($F_{ST} = 0.163$; $p<0.001$) was only slightly lower than that of the total Gulf St Vincent data set. This indicated that most of the genetic variation was derived from between locations and not from between coastlines.

Estimates of gene flow indicated very low levels of exchange between locations ($N_em = 1.08$; range 0.66 to 1.72 immigrants per generation). Excluding the geographically furthest location (Hallett Cove) from the analysis still resulted in N_em values ($N_em = 1.28$; range 0.9 to 2.01 immigrants per generation) similar to other species of marine gastropods with direct development (Hoskin 1996).

Discussion

The genetic population structure of *L. vinosa* was consistent with the predicted effects of recruitment via sexually produced offspring with a low dispersal ability. Genotypic frequencies within samples were for the most part in good agreement with expectations for Hardy-Weinberg equilibrium. Only *Acon-1* at Stansbury exhibited a departure from Hardy-Weinberg expectations, attributable to a significant heterozygote deficit.

Heterozygote deficiency is a common phenomenon in molluscs (Zouros & Foltz 1984; Volckaert & Zouros 1989). Possible explanations include typing errors, non-random mating, selection, the presence of null alleles and the Wahlund effect (Singh & Green 1984; Hare *et al.* 1996). As the phenotypes for *Acon-1* were clear and readily resolved, typing errors were improbable. Non-random mating due to inbreeding or assortative mating was also considered unlikely, because either of these processes would be expected to give heterozygote deficiencies for all loci in that sample. A common explanation for heterozygote deficiency in molluscs is selection (Zouros & Foltz 1984). However, it is generally restricted to species with high differential mortality (Richardson *et al.* 1986), such as those with long larval phases (e.g. Singh & Green 1984). As *L. vinosa* lacks a planktonic phase it is unlikely that this deficit is the result of selective forces.

Hence, either the presence of null alleles (Milkman & Beaty 1970) or the Wahlund effect (e.g. Koehn *et al.* 1976; Johnson & Black 1984) seem the most likely candidates to explain the observed deficit. Without further analysis, preferably at the DNA level, we cannot discount either of these hypotheses. The absence of linkage disequilibrium coupled with high levels of genetic variation indicates that none of the populations have recently passed through a significant population bottleneck.

In contrast to several studies of marine gastropods with direct development (Johnson & Black 1984; Grant & Utter 1988), intrapopulation allelic frequencies for *L. vinosa* over a range of 500 m were homogeneous. This implies that panmixia prevails over this scale. As this species has no planktonic larval dispersive stage, possible explanations for this genetic cohesion include both adult migration and passive dispersal. The contribution of adult migration to gene flow is likely to be small given the sedentary nature of this species. A possible dispersal mechanism capable of maintaining gene flow levels over this scale is floating. Martel & Chia (1991) found that gastropods similar in size to juvenile *L. vinosa* floated in the water column and, coupled with the ability of this species to breed throughout the year (Synnot 1980), potentially provides a constant source of migrants. Size and weight constraints, vulnerability to predation or starvation and possible advection away from suitable habitats, suggest that floating is likely to be a local-scale dispersal mechanism (Highsmith 1985; Martel & Chia 1991).

In contrast to the homogeneity within locations, there was widespread variation in allelic frequencies for all polymorphic loci between samples separated by more than 10 km. Mean genetic distance values were similar to those for other gastropods with non-pelagic larvae over a similar geographic range (Day & Bayne 1988). Multilocus heterogeneity between samples is

consistent with population subdivision rather than locus-specific effects such as selection (Richardson *et al.* 1986).

Examination of the distributional pattern of allelic variation gives further indications of the degree of isolation between locations. She Oak Flat has an allele (*Acon-1*^{c}) not found elsewhere. This suggests that gene flow between this location and its neighbours, only 13 km distant in the case of Pine Point, is very low or non-existent and has not occurred for a period of time required for alternative allelic accumulations (Larson *et al.* 1984). The pattern of allele frequency distributions is disjunct, there being no clear correlation between genetic and geographic distance.

Our data suggest that the dispersal ability of *L. vinosa* is insufficient to prevent genetic differentiation at locations separated by more than 10 km. This interpretation is supported by very low levels of calculated gene flow, which at $N_em < 1$ can be considered insufficient to prevent differential between locations due to random genetic drift (Slatkin 1985). The genetic population structure of this species is consistent with the discrete subpopulation model of Richardson *et al.* (1986), the population consisting of a series of subpopulations within which mating occurs at random. These subpopulations are separated from one another by restricted dispersal that allows very little migration between them. Our data indicate that the size of subpopulations is somewhere between 500 m and 10 km. Further investigations, at a finer scale, would give a more accurate estimate of the neighbourhood size of subpopulations.

If this population model is correct, then how does *L. vinosa* maintain a wide geographical range? The most likely explanation is rafting, which has been suggested as the main mechanism of long range dispersal in many species of brooding invertebrates (Highsmith 1985; Jackson 1986; Johannesson 1988; Martel & Chia 1991). *L. vinosa* is found in the intertidal region where rafting agents such as drift wood and algal wrack abound. Furthermore, the newly-hatched juveniles of this species are small enough to float on the water surface (see Martel & Chia 1991), increasing the probability of rafting because they are more likely to encounter rafting agents (Highsmith 1985). However, the level of dispersal by rafting, while able to found new populations, is insufficient to maintain allele frequency homogeneity between widely separated locations.

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References

Burton, R. S. 1983. Protein polymorphism and genetic differentiation of marine invertebrate populations. *Marine Biology Letters* **4:** 193-206.

Carvalho, G. R., & Piertney, S. B. 1997. Interspecific comparisons of genetic population structure in members of the *Jaera albifrons* species complex. *Journal of the Marine Biological Association of the United Kingdom* **77:** 77-93.

Crisp, D. J. 1978. Genetic consequences of different reproductive strategies in marine invertebrates. Pp. 257-273. In: Battaglia, B. & Beardmore, J. A.*Marine Organisms: Genetics, Ecology and Evolution*. Plenum Press, New York.

Day, A. J., & Bayne, B. L. 1988. Allozyme variation in populations of the dog-whelk *Nucella lapillus* (Prosobranchia: Muricacea) from the South West peninsula of England. *Marine Biology (Berlin)* **99:** 507-513.

Dell, R. K. 1972. Antarctic benthos. *Advanced Marine Biology* **10:** 1-216.

Endler, J. A. 1973. Gene flow and population differentiation. *Science* **179:** 243-250.

Grant, W. S., & Utter, F. M. 1988. Genetic heterogeneity on different geographical scales in *Nucella lamellosa* (Prosobranchia, Thaididae). *Malacologia* **28:** 275-287.

Hare, M. P., Karl, S. A., & Avise, J. C. 1996. Anonymous nuclear DNA markers in the American oyster and their implications for the heterozygote deficiency phenomenon in marine bivalves. *Molecular Biology and Evolution* **13:** 334-345.

Hedgecock, D. 1986. Is gene flow from pelagic larval dispersal important in the adaptation and evolution of marine invertebrates? *Bulletin of Marine Science* **39:** 550-564.

Highsmith, R. C. 1985. Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. *Marine Ecology Progress Series* **25:** 169-179.

Hill, W. G. 1974. Estimation of linkage disequilibrium in randomly mating populations. *Heredity* **33:** 229-239.

Hoskin, M. G 1997. Effect of contrasting modes of larval development on the genetic structures of populations of three species of prosobranch gastropods. *Marine Biology (Berlin)* **127:** 647-656.

Jackson, J. B. C. 1986. Modes of dispersal of clonal benthic invertebrates: consequences for species' distribution and genetic structure of local populations. *Bulletin of Marine Science* **39:** 588-605.

Janson, K. 1987. Allozyme and shell variation in two marine snails (Littorina, Prosobranchia) with different dispersal abilities. *Biological Journal of the Linnean Society* **30:** 245-256.

Janson, K., & Ward, R. D. 1984. Microgeographic variation in allozyme and shell characters in *Littorina saxatilis* Olivi (Prosobranchia: Littorinidae). *Biological Journal of the Linnean Society* **22:** 289-307.

Johannesson, K. 1988. The paradox of Rockall: why is a brooding gastropod (*Littorina saxatiliis*) more widespread than one having a planktonic larval dispersal stage (*L. littorea*)? *Marine Biology (Berlin)* **99:** 507-513.

Johnson, M. S., & Black, R. 1984. The Wahlund effect and the geographical scale of variation in the limpet *Siphonaria* sp. *Marine Biology (Berlin)* **79:** 295-302.

Koehn, R. K., Milkman, R., & Mitton, J. 1976. Population genetics of marine pelecypods. IV. Selection , migration and genetic differentiation in the blue mussel, *Mytilus edulis*. *Evolution* **30:** 2-32.

Larson, A., Wake, D. B., & Yanev, K. P. 1984. Measuring gene flow among populations having high levels of genetic fragmentation. *Genetics* **106:** 293-308.

Levene, H. 1949. On a matching problem arising in genetics. *Annual in Mathematical Statistics* **20:** 91-94.

Macpherson, J.H. & Gabriel, C.J. 1962. *Marine Molluscs of Victoria.* Melbourne University Press, Melbourne.

Martel, A., & Chia, F. 1991. Drifting and dispersal of small bivalves and gastropods with direct development. *Journal of Experimental Marine Biology and Ecology* **150:** 131-147.

Milkman, R., & Beaty, L. D. 1970. Large-scale electrophoretic studies of allelic variation in *Mytilus edulis*. *Biological Bulletin* **139:** 4-30.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* **89:** 583-590.

O'Foighil, D. 1989. Planktotrophic larval development is associated with a restricted geographic range in *Lasaea*, a genus of brooding, hermaphroditic bivalves. *Marine Biology (Berlin)* **103:** 349-358.

Ovenden, J. R., Brasher, D. J., & White, R. W. G 1992. Mitochondrial DNA analyses of the red rock lobster (*Jasus edwardsii*) supports an apparent absence of population subdivision throughout Australasia. *Marine Biology (Berlin)* **112:** 319-326.

Parsons, K. E. 1996. The genetic effects of larval dispersal depend on spatial scale and habitat characteristics. *Marine Biology (Berlin)* **126:** 403-414.

Rice, W. R. 1989. Analysing tables of statistical tests. *Evolution* **43:** 223-225.

Richardson, B. J., Baverstock, P. R., & Adams, M. 1986. *Allozyme Electrophoresis: A Handbook of Animal Systematics and Population Structure*. Academic Press, Sydney.

Scheltema, R. S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biological Bulletin (Woods Hole)* **175:** 218-229.

Scheltema, R. S. 1986. On dispersal and planktonic larvae of benthic invertebrates: an electic overview and summary of problems. *Bulletin of Marine Science* **39:** 290-322.

Siegel, S. 1956. *Non Parametric Statistics for the Behavioural Sciences*. McGraw-Hill Kogakusha, Tokyo.

Singh, S.M. & Green, R.H. 1984. Excess of allozyme homozygosity in marine molluscs and its possible biological significance. *Malacologia* **25:** 569-581.

Slatkin, M. 1985. Gene flow in natural populations. *Annual Review in Ecological Systematics* **16:** 393-430.

Smith, B.J., Black, J.H. & Shepherd, S.A. 1989. Molluscan egg masses and capsules. in: Shepherd. S.A. & Thomas, I.M. (eds.). *Marine Invertebrates of Southern Australia, Part II.* pp. 841-862. South Australian Government Printing Divison, Adelaide.

Snyder, T. P., & Gooch J. L. 1973. Genetic differentiation in *Littorina saxatilis* (Gastropoda). *Marine Biology (Berlin)* **22:** 177-182.

Sokal, R. R., & Sneath, P. H. A. 1963. *Principles of Numerical Taxonomy*. W. H. Freeman, San Francisco.

Swofford, D. L., & Selander, R. B. 1981. BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. *Journal of Heredity* **72:** 281-283.

Synnot, R. N. 1980. The egg capsules of *Lepsiella vinosa* (Lamarck 1882) (Muricidae: Thaidinae). *Journal of the Malacological Society of Australia* **4:** 209-211.

Volckaert, F., & Zouros, E. 1989. Allozyme and physiological variation in the scallop *Placopecten magellanicus* and a general model for the effects of heterozygosity on fitness in marine molluscs. *Marine Biology (Berlin)* **103:** 51-61.

Waples, R. S. 1987. A multispecies approach to the analysis of gene flow in marine shore fishes. *Evolution* **41:** 385-400.

Weir, B. S. 1990. Genetic Data Analysis. Sinauer, Sunderland, Massachusetts.

Weir, B. S., & Cockerham, C. C. 1984. Estimating F-statistics for the analysis of population structure. *Evolution* **38:** 1358-1370.

Wilson, B.R & Gillett, K. 1974. *Australian Shells*. Revised edition. A. H. & A. W. Reed, Sydney.

Wright, S. 1978. *Evolution and the Genetics of Populations: Variability Within and Among Populations*. University of Chicago Press, Chicago.

Zouros, E., & Foltz, D. W. 1984. Possible explanations of heterozygote deficiency in bivalves molluscs. *Malacologia* **25:** 583-591.

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Some Pectinoidea (Mollusca: Bivalvia: Propeamussiidae, Pectinidae) of the Red Sea

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Abstract

The report is based on a collection of 344 samples of pectinoids from the Red Sea and adjacent waters. Four species of Propeamussiidae and 18 species of Pectinidae were recognized. One pectinid taxon, *Mirapecten yaroni*, is undescribed. Three taxa are new pectinid records for the area: *Delectopecten musorstomi* Poutiers, 1981, *Glorichlamys quadrilirata* (Lischke, 1870), and *Mimachlamys andamanica* (Preston, 1908). *Gloripallium pallium* (Linnaeus, 1758) is recorded as living in the area for the first time. Lectotypes are designated for *Similipecten eous* (Melvill *in* Melvill & Standen, 1907) *Decatopecten flabelloides* (Reeve, 1852), *Coralichlamys madreporarum* (G.B. Sowerby 2nd., 1842) and *Semipallium crouchi* (Smith, 1892). Type localities of 20 taxa and the depository of type material for 19 taxa are given. All taxa are figured and extensive synonymy is presented. Intraspecific variation of most taxa is described. The total geographic distribution of each taxon is outlined. The following taxa may be endemic for the Erythrean subprovince: Propeamussiidae: *Parvamussium formosum* (Melvill *in* Melvill & Standen, 1907), *P. siebenrocki* (Sturany, 1901), and *P. thyrideum* (Melvill *in* Melvill & Standen, 1907); Pectinidae: *Pecten erythraeensis* G.B. Sowerby 2nd, 1842, *Gloripallium maculosum* (Forsskål, 1775), *Laevichlamys superficialis* (Forsskål, 1775). Two taxa: *L. superficilalis* (Forsskål, 1775) and *Mimachlamys senatoria* (Gmelin, 1791) are recorded from the Little Bitter Lake, Suez Canal. None of the taxa dealt with has migrated into the Mediterranean Sea.

Key words: Pectinoidea, Propeamussiidae, Pectinidae, taxonomy, zoogeography, Red Sea, NW Indian Ocean.

Introduction

The present paper is based on various collections of the families Propeamussiidae and Pectinidae from the Red Sea, the Gulf of Aden and a few samples from adjacent waters; most of the material originates from the Gulf of Aqaba.

Through the courtesy of the late professor Al. Barash a large collection of Pectinoidea, mainly kept at the Department of Zoology, Tel Aviv University, was entrusted to J. Knudsen for examination. Most of the material was identified, selected specimens photographed and a draft manuscript worked out. Following a visit of H.H. Dijkstra to the Zoological Museum, Copenhagen, it was decided that the latter should join the project and that the scope of the paper should be considerably extended. In addition numerous samples from H. Dijkstra's private collection were included.

The material comprises 4 taxa of Propeamussiidae and 18 taxa of Pectinidae, obtained at depths between 0 and 740 meters. It consists of material from the following collections:

1) Zoological Museum of the University of Tel Aviv: Samples registered prior to 1982 are marked NS; samples registered after 1982 are marked MO. This material was collected between 1966 and 1971. Samples marked ISRSE were collected in 1965 during the Israel South Red Sea Expedition.
2) Material kept at the Department of Zoology, The Hebrew University, Jerusalem (HUJ).
3) The private collection of H.H. Dijkstra (HD).
4) Zoological Museum, The University, Copenhagen (ZMUC).

In the sections "Material examined" the distinction between live-collected "live specimens", united (articulated) valves and separate valves has been made. By far the major part of the material consists of separate valves.

Type specimens (*) of the present species discussed are examined, or not seen (-).

Abbreviations

AIM, Auckland Institute and Museum, Auckland
AMS, Australian Museum, Sydney
BMNH, The Natural History Museum, London
HD, H.H. Dijkstra collection, Sneek, The Netherlands
HUJ, Hebrew University of Jerusalem, Jerusalem
IGPS, Institute of Geology and Palaeontology, Tohoku University, Sendai
ISRSE, Israel South Red Sea Expedition (specimens in the ZMTAU)
LSL, The Linnean Society of London, Burlington House, London
MNHN, Muséum National d'Histoire Naturelle, Paris
MNHNS, Museo Nacional de Historia Natural, Santiago
MO, ZMTAU collection numbers after 1982
NHMW, Naturhistorisches Museum Wien, Vienna
NM, Natal Museum, Pietermaritzburg
NMW, National Museum of Wales, Cardiff
NNM, Nationaal Natuurhistorisch Museum, Leiden
NS, ZMTAU collection numbers prior 1982
TMAG, Tasmanian Museum and Art Gallery, Hobart
UMZC, University Museum of Zoology, Cambridge, U.K.
UUZM, Uppsala University Zoological Museum, Uppsala
WPUR, Wilhelm Pieck Universität, Rostock
ZMA, Zoological Museum, University of Amsterdam
ZMB, Museum für Naturkunde, Humboldt-Universität, Berlin
ZMUC, Zoological Museum, University of Copenhagen
ZSI, Zoological Survey of India, New Alipur, Calcutta
ZMTAU, Tel Aviv University, Tel Aviv
D, diameter
fr., fragment
H, height
L, length
lv, left valve
rv, right valve
spm(s)., an articulated specimen(s)
stn., station
v, valve

Systematics

Superfamily **PECTINOIDEA** Wilkes, 1810 [emend. Waller, 1978]
Family **PROPEAMUSSIIDAE** Abbott, 1954
Genus **Parvamussium** Sacco, 1897

Parvamussium Sacco, 1897a: 102.
Type species (by original designation): *Pecten (Pleuronectes) duodecimlamellatus* Bronn, 1832; Upper Miocene, northern Italy.
For synonymy, diagnosis, distribution and remarks see Dijkstra (1995: 25).

Parvamussium formosum (Melvill *in* Melvill & Standen, 1907)
(Plate 2, figs. 5-8)

**Amussium formosum* Melvill *in* Melvill & Standen, 1907: 807, pl. 55, figs. 7, 7a.
Propeamussium cf. *scitulum* (Smith).- Oliver, 1992: 70, 73, pl. 12, fig. 4, text-fig. 5.
Parvamussium formosum.- Rombouts, 1991: 67.

Type material: Two syntypes (2 rv) BMNH 1907.5.3.50, 26 syntypes NMW 1955.158.674. Several syntypes deposited in other museums (Dijkstra, personal observation).

Type locality: Persian Gulf, Gulf of Oman, 24°58'N, 56°54'E, 156 fathoms [= 285 m].

Material examined: The type material. RED SEA: Opposite Elat, 180m, 4 v, 6.ix.1966, MO 28451; Opposite Elat, 180m, 1 v, 6.ix.1966, MO 28472; Opposite Elat, 180-200m, 20 v, 6.ix.1966, MO 28461; Opposite Elat, 180-200m, 2 v, 6.ix.1966, MO 28452; Elat, opposite Marine Lab., 400-450m, 1 v, 6.ix.1966, MO 28473; Elat, opposite Marine Lab., 215m, 5 v, 6.ix.1966, MO 28470; Opposite Elat, 80m, 4 v, 7.ix.1966, MO 28475; Opposite Elat, 62-80m, 7 v, 7.ix.1966, MO 28467; off Gerivat Farun, 50m, 2 v, 21.viii.1968, MO 28448; Elat, opposite Old Port, 121m, 20 v, 10.ix.1968, MO 28460; Elat, opposite Old Port, 121m, 15 v, 10.ix.1968, MO 28462; Elat, opposite New Port, 220m, 15 v, 16.ix.1968, MO 28454; Elat, opposite New Port, 220m, 3 v, 16.ix.1968, MO 28453; Elat, opposite Zarhin Plant., 167m, ca. 140 v, 16.ix.1968, MO 28449; Elat, opposite Zarhin Plant., 167m, ca. 125 v, 16.ix.1968, MO 28450; Elat, opposite Zarhin Plant., 167m, 2 v, 16.ix.1968, MO 28447; off Mersat Abu Samra, 55m, 1 v, 6.x.1969, MO 28469; off Mersat Abu Samra, 50m, 2 v, 6.x.1969, MO 28471; off Mersat Abu Samra, 140m, 67 v, 6.x.1969, MO 28459; off Murach, 91m, 2 v, 6.x.1969, MO 28463; off Nuweiba el Tarabin, 137-146m, ca. 1000 v, 8.x.1969, MO 28537; off Nuweiba el Tarabin, 150m, 1 v, 8.x.1969, MO 28477; off Nuweiba el Museina, 330-400m, 1 v (fragment), 8.x.1969, MO 28457; off Nuweiba el Museina, 274-300m, 3 v, 8.x.1969, MO 28456; off Wadi Murach, 80m, 1 v, 9.x.1969, MO 28445; off Elat, 242m, 10 v, 17.xi.1969, MO 28446; Elat, opposite Electric Plant., 320m, 2 v, 9.ii.1970, MO 28464; Elat, opposite Electric Plant., 320m, 1 v, 9.ii.1970, MO 28476; Elat, opposite Marine Lab., 600m, 2 v, 9.ii.1970, MO 28468; Elat, opposite New Port, 270m, 45 v, 13.ii.1970, MO 28465; Elat, opposite New Port, 170-270m, 19 v, 13.ii.1970, MO 28458; Elat, opposite New Port, 170-270m, 18 v, 13.ii.1970, MO 28466; Elat, opposite New Port, 270m,

10 v, 13.ii.1970, MO 28444; Elat, opposite Old Port, 300-420m, 4 v, 13.ii.1970, MO 28474; Elat, opposite Old Port, 300-420m, 11 v, 13.ii.1970, MO 28455; Gulf of Aqaba, 410m, several v, HUJ 706; Gulf of Aqaba, 700-740m, 4 v, HUJ 787; Elat, 300m, several v, HUJ 20692; Gulf of Aqaba, 192m, several v, HUJ 20696; Elat, 280-300m, 6 v, HUJ 21495; Gulf of Aqaba, 30-35m, 3 v, HUJ 35594; Gulf of Aqaba, 30-35m, HUJ 35597; Elat, harbour, 7 v, HUJ 35603; Dahlak Archipelago, 15°18'N, 40°23'E, 55m, 1 v, 16.x.1965, ISRSE 1965-0153.

Distribution: Northwestern and western Indian Ocean, Red Sea and Persian Gulf. Sublittoral to bathyal depths, living on soft substrates.

Remarks: Most Red Sea specimens are finely radially striated only near the anterior and posterior margins, and smooth on the central part of the disc. The internal ribs vary from 8-11, sometimes with rudimentary intercostal radial riblets. The right valve is smooth or finely sculptured commarginally. Perhaps only a smooth form of *Parvamussium siebenrocki* (Sturany, 1901).

For description of the present species see Oliver (1992: 73 [as *Propeamussium* cf. *scitulum*]).

Parvamussium siebenrocki (Sturany, 1901)
(Plate 1, figs. 1-4)

**Amussium siebenrocki* Sturany, 1901: 269, pl. 4, figs. 5-8.
Amusium siebenrocki.- Cox, 1929: 207.
Parvamussium siebenrocki.- Oliver, 1982: 2.
Parvamussium siebenrocki.- Bosch, Dance, Moolenbeek & Oliver, 1995: 232, fig. 1011.
Propeamussium (Parvamussium) siebenrocki.- Oliver, 1992: 70, 73, pl. 12, figs. 3a-3b, text-figs. 7a-b.

Type material: Figured syntype (lv) (Sturany, 1901: pl. 4, figs. 7-8) (NHMW 84.355), 8 syntypes (2 lv + 6 rv) NHMW 84.177.

Type locality: 'Pola ' stn. 72, Red Sea, near Shadwan Island, 27°25'N, 34°30'E, 1082 m, yellowish muddy sand, 2 April 1896.

Material examined:
The type material. RED SEA: Elat, off Marine Lab., MO 28545, 215m, 9 v, 6.ix.1966; Elat, off Marine Lab., MO 28546, 400-450m, 2 v, 6.ix.1966; Elat, off Marine Lab., MO 28549, 215m, 4 v, 6.ix.1966; Elat, off Marine Lab., MO 28543, 600m, 2 v, 6.ix.1966; Elat, opposite Old Port, MO 28539, 121m, 7 v, 10.ix.1968; Elat, opposite Oil Port, MO 28540, 300-420m, 1 v, 13.ii.1970; Elat, opposite Oil Port, MO 28550, 344m, 2 v, 10.ix.1968; Elat, opposite Oil Port, MO 28544, 350m, 19 v, 16.ix.1968; Elat, opposite Oil Port, MO 28548, 350m, 8 v, 16.ix.1968; Elat, opposite Ras Taba, MO 28541, 690m, 3 v, 17.xi.1969; Elat, opposite Lighthouse, MO 28542, 300m, 1 v, 11.ii.1970; Elat, opposite Ras Taba, MO 28551, 700m, 2 v, 12.ii1970; Elat, 280-300m, 1lv, HUJ 21494; Elat, 250-300m, HUJ 35588; S of

Nuweiba, MO 28538, 550-700m, 25 v, 8.x.1969; S of Nuweiba, MO 28547, 550m, 16 v, 8.x.1969.

Distribution: Red Sea, Gulf of Aden, Arabian Sea and Persian Gulf to northern eastcoast of South Africa. Sublittoral to bathyal depths, living on soft substrates (mud, muddy sand).

Remarks: As mentioned by Sturany (1901: 269) internal ribs are supplemented with rudimentary interstitial riblets in some specimens, but generally are 10 in number. The external sculpture of the left valve is variable; some specimens lack commarginal lamellae, some are more cancellated.

For description of the present species see Oliver (1992: 73).

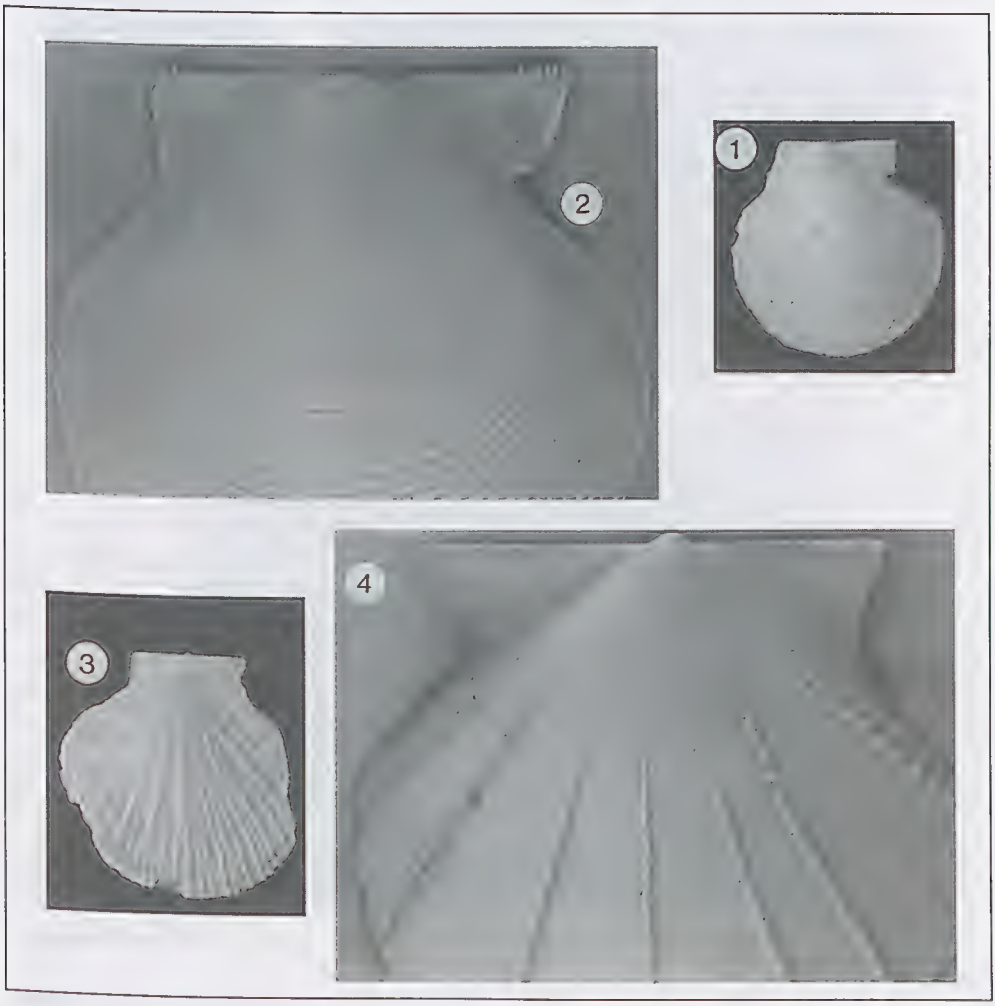


Plate 1.

Figures 1-4. *Parvamussium siebenrocki* (Sturany, 1901). **1.** TAU-MO 28547, S of Nuweiba, 550m, H 6.0mm, rv, exterior. **2.** idem, H 5.5mm, rv, exterior. **3.** TAU-MO 28539, Elat, opp. Old Port, 121m, H 10.7mm, lv, exterior. **4.** idem, H 6.0mm, lv, exterior.

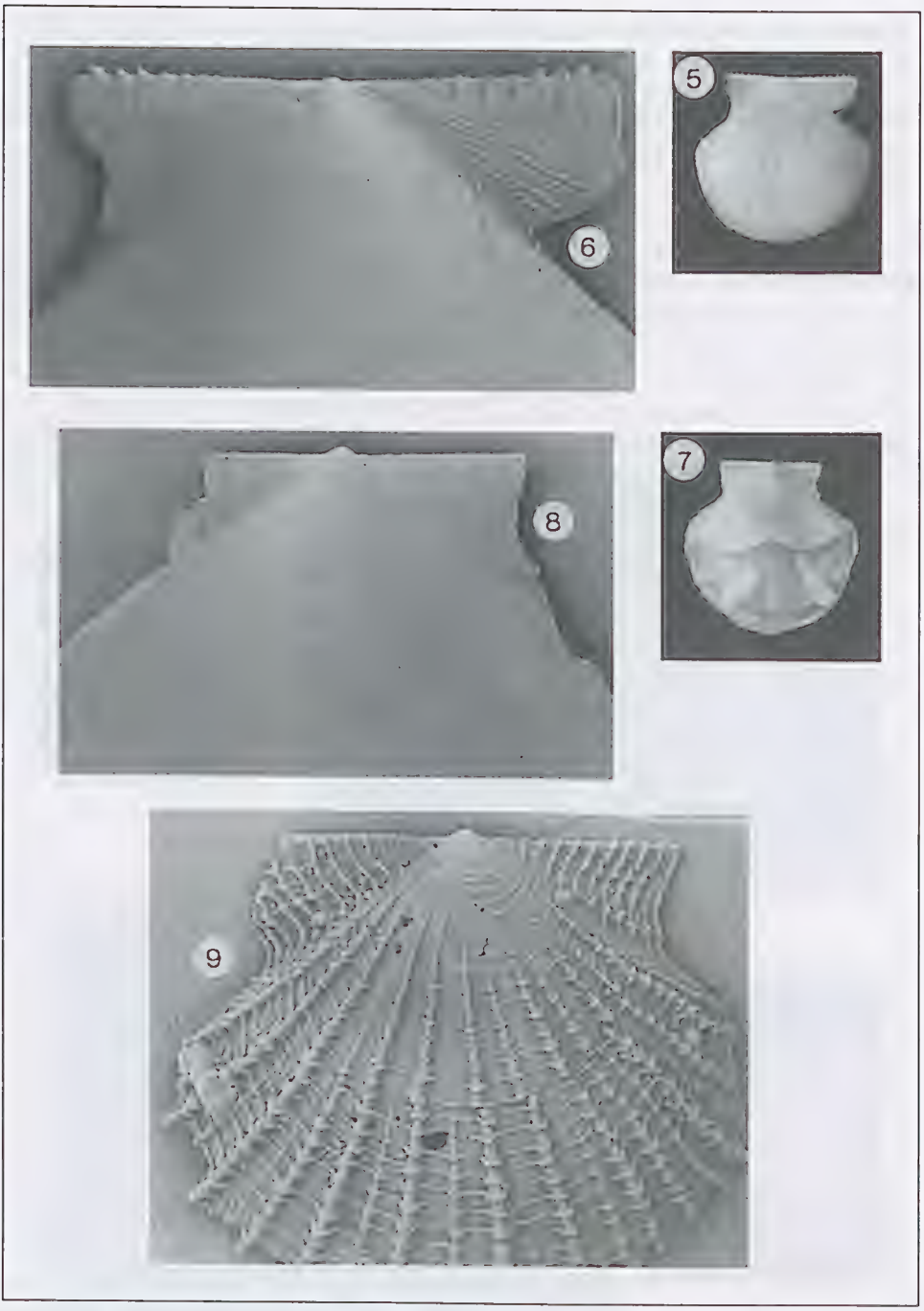


Plate 2.

Figures 5-8. *Parvamussium formosum* (Melvill *in* Melvill & Standen, 1907). **5.** TAU-MO 28450, Elat, opp. Zarkin Plant., 167m, H 11.0mm, rv, exterior. **6.** idem, H 10.6mm, rv, exterior. **7.** TAU-MO 28460, Elat, opp. Old Port, 121m, H 9.9mm, lv, exterior. **8.** idem, H 9.6mm, lv, exterior. **9.** *Parvamussium thyrideum* (Melvill *in* Melvill & Standen, 1907). TAU-MO 28553, off Nuweiba el Tarabin, 137-146m, H 3.0mm, lv, exterior.

Parvamussium thyrideum (Melvill *in* Melvill & Standen, 1907)
(Plate 2, fig. 9)

**Pecten thyrideus* Melvill *in* Melvill & Standen, 1907: 809, pl. 55, figs. 10-10a.
Parvamussium thyrideus.- Oliver, 1982: 2; Bosch, Dance, Moolenbeek & Oliver, 1995: 232.
Pecten thyrideus.- Trew, 1987: 67.
Propeamussium (Parvamussium) thyrideum.- Oliver, 1992: 70, 73, text-fig. 6.

Type material: Figured syntype (valve) and 3 other syntypes (valves) BMNH 1907.5.33-37; 7 syntypes (valves) NMW 1955.158.679. Several syntypes are distributed to other museums (Dijkstra, personal observation).

Type locality: Gulf of Oman, 24°58'N, 56°54'E, 156 fathoms [= 285 m], shell-sand.

Material examined: The type material. RED SEA: Elat, opposite New Port, MO 28552, 220m, 1 v (fragment), 16.ix.1968; Elat, opposite Electric Plant., MO 28554, 320m, 2 v, 9.ii.1970; off Nuweiba el Tarabin, MO 28553, 137-146m, 1 v, 8.x.1969.

Distribution: Red Sea, Gulf of Oman, Arabian Sea and Persian Gulf. Sublittoral to bathyal depths, living on soft substrates (sand and shellgrit).

Remarks: Some specimens have internal irregularly arranged rudimentary radial riblets near the periphery; these are absent in others.

For description of the present species see Oliver (1992: 73).

Genus **Similipecten** Winckworth, 1932

Similipecten Winckworth, 1932: 241, 250.
Type species (by original designation): *Pecten similis* Laskey, 1811; Recent, E Atlantic.

Diagnosis: A free-living, small to medium sized, compressed propeamussiid; shell semi-orbicular, generally transparent, slightly opaque, smooth or sculptured with minute commarginal growthlines or fine striae; anterior and posterior auricles well developed, nearly equal in length; byssal notch moderately slight; no ctenolium; cardinal crura rather broad.

Distribution: Eocene - Recent (Hertlein, 1969: N354); Arctic to tropical Atlantic, NW Indian Ocean to Indo-West Pacific; littoral (Arctic and boreal region) to bathyal depths.

Remarks: Hertlein (1969: N354) placed *Similipecten* Winckworth in the *Eburneopecten* group of Pectinidae as a synonym of *Palliolum (Delectopecten)* Stewart, 1930. However, Waller (1984: 213) treated *Similipecten* as a valid genus of the Propeamussiidae.

Similipecten eous (Melvill *in* Melvill & Standen, 1907)
(Plate 3, figs. 10-11)

**Pecten eous* Melvill *in* Melvill & Standen, 1907: 808, pl. 55, fig. 9.
Delectopecten eous.- Oliver, 1982: 3.
Pecten eous.- Trew, 1987: 38.
Similipecten eous.- Oliver, 1992: 74, text-figs. 9a-b; Bosch, Dance, Moolenbeek & Oliver, 1995: 232.

Type material: Lectotype (Melvill & Standen, 1907: pl. 55, fig. 9) here designated (BMNH 1907.5.3.18). Two paralectotypes (valves and fragments): BMNH 1907.5.3.19-20. Seventeen paralectotypes (valves): NMW 1955.158.673. Other paralectotypes in several other museums (Dijkstra, personal observation).

Type locality: Gulf of Oman, 24°58'N, 56°54'E, 285m, shell-sand.

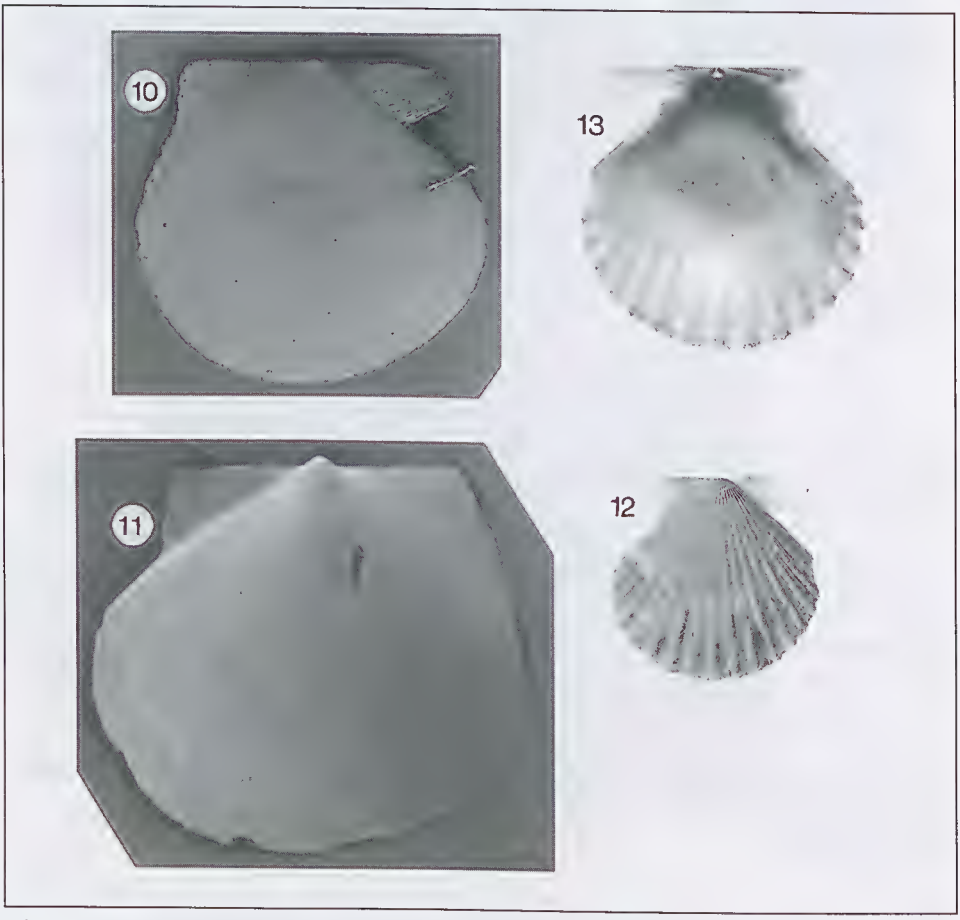


Plate 3.
Figures 10-11. *Similipecten eous* (Melvill *in* Melvill & Standen, 1907). **10.** TAU-MO 28482, Elat, off Zarkin Plant., 167m, H 2.8mm, rv, exterior. **11.** idem, H 3.8mm, lv, exterior. **12-13.** *Cryptopecten nux* (Reeve, 1853). **12.** TAU-MO 28501, off Elat, 40-50m, H 13.6mm, rv, exterior. **13.** idem, rv, interior.

Material examined: The type material. RED SEA: off Elat, MO 28484, 180-200m, 3 v, 6.ix.1966; Elat, off Marine Lab., MO 28497, 215m, 14 v, 6.ix.1966; Elat, off Marine Lab., MO 28483, 400-450m, 1 v, 6.ix.1966; Elat, off Marine Lab., MO 28481, 215m, 11 v, 6.ix.1966; Elat, off Marine Lab., MO 28499, 600m, 2 v, 6.ix.1966; off Elat, MO 28492, 80m, 4 v, 7.ix.1966; Elat, opposite New Port, MO 28493, 220m, 10 v, 16.ix.1968; Elat, opposite New Port, MO 28496, 220m, 5 v, 16.ix.1968; Elat, off Zarhin Plant., MO 28494, 167m, 1 v, 16.ix.1968; Elat, off Zarhin Plant., MO 28482, 167m, 53 v, 16.ix.1968; Elat, opposite Oil Port, MO 28479, 350m, 2 v, 16.ix.1968; Elat, opposite Oil Port, MO 28480, 350m, 2 v, 16.ix.1968; off Nuweiba el Tarabin, MO 28488, 150m, 1 v, 8.x.1969; off Wadi Murach, MO 28490, 80m, 1 v, 9.x.1969; Elat, opposite Ras Taba, MO 28495, 690m, 3 v, 17.xi.1969; Elat, MO 28486, 242m, 2 v, 17.xi.1969; Elat, opposite Marine Lab., MO 28485, 600m, 1 v, 9.ii.1970; Elat, opposite New Port, MO 28491, 270m, 10 v, 13.ii.1970; Elat, opposite New Port, MO 28489, 270m, 2 v, 13.ii.1970; Elat, opposite New Port, MO 28487, 270m, 3 v, 13.ii.1970; Elat, opposite Old Port, MO 28498, 300-420m, 3 v, 13.ii.1970; Gulf of Aqaba, 4 v, HUJ 20697; Gulf of Aqaba, 1 v, HUJ 35593; Elat, harbour, 5 v, HUJ 35604.

Distribution: Red Sea, Gulf of Oman, Arabian Sea, Persian Gulf and Indonesia (Dijkstra, 1991b: 23). In sublittoral to bathyal zone, living on soft substrates (mud, muddy sand, shellgrit).

Remarks: The present species is morphologically closely allied to *Similipecten similis* (Laskey, 1811) from the eastern Atlantic and Mediterranean Sea. The latter species is more colourful and larger (up to 6mm high).

For description of the present species see Dijkstra (1991b: 23).

Family **PECTINIDAE** Wilkes, 1810
Subfamily **CAMPTONECTINAE** Habe, 1977
Genus **Delectopecten** Stewart, 1930

Delectopecten Stewart, 1930: 118.
Type species (by original designation): *Pecten (Pseudamusium) vancouverensis* Whiteaves, 1893; living, Forward Inlet, Quatsino Sound, Vancouver Island, 18-37m. For diagnosis, distribution and remarks see Dijkstra (1995: 50).

Delectopecten musorstomi Poutiers, 1981
(Plate 7, figs. 31-32)

**Delectopecten musorstomi* Poutiers, 1981: 331, pl. 1, figs. 2-3.
Delectopecten musorstomi.- Dijkstra, 1991b: 26; 1995: 53, figs. 69-70.

Type material: Holotype MNHN [not registered].

Type locality: Philippines, N of Lubang, 13°57'N, 120°16.5'E, 150-159m, live, sediments (gravel, coral rubble), 21.iii.1976.

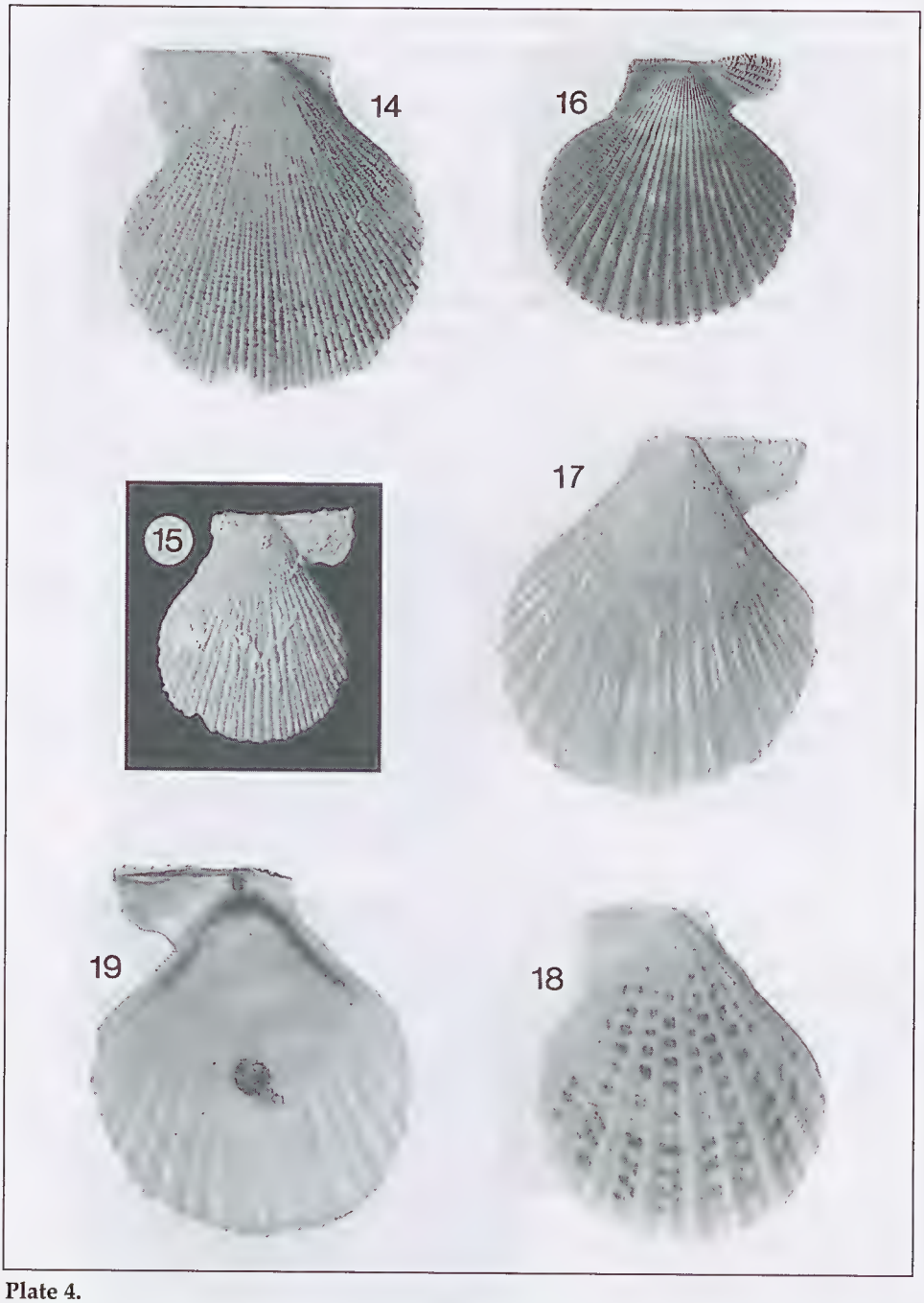


Plate 4.

Figures 14-15. *Mimachlamys andamanica* (Preston, 1908). **14.** TAU-MO 28466, Elat, opp. New Port, 170-270m, H 8.3mm, lv, exterior. **15.** TAU-MO 28441, Elat, off Old Port, 121m, H 13.0mm, rv, exterior. **16.** *Mimachlamys senatoria* (Gmelin, 1791). ISRSE/1965-2544, Dahlak Archipelago, 36m, H 45.5mm, rv, exterior. **17-19.** *Laevichlamys rubromaculata* (G.B. Sowerby 2nd, 1842). **17.** ZMUC, Elat, H 29.9mm, rv, exterior. **18.** idem, H 27.9mm, lv, exterior. **19.** idem, H 29.9mm, rv, interior.

Material examined: The type material. RED SEA: Elat, opposite Old Port, 121m, 1 v, 10.ix.1968, MO 28508; Elat, opposite Oil Port, 344m, 1 v, 10.ix.1968, MO 28550; Elat, opposite Oil Port, 350m, 1 v (fragment), 16.ix.1968, MO 28532.

Distribution: So far Red Sea, Philippines and New Caledonia. Sublittoral depths, living on soft sediments.

Remarks: Knudsen (1967: 282) mentioned *Delectopecten alcocki* (Smith, 1904) from the Gulf of Aden. That species differs from *D. musorstomi* in lacking the radial riblets on the left valve and in the microscopic sculpture of antimarginal striae ('*Camptonectes*' sculpture) on both valves.

For description of the present species see Dijkstra (1995: 53).

Tribe **DECATOPECTININI** Waller, 1986
Genus **Decatopecten** [Rüppell] G.B. Sowerby 2nd, 1839

Decatopecten [Rüppell] G.B. Sowerby 2nd, 1839: 37, fig. 172.
Type species (by monotypy): *Ostrea plica* Linnaeus, 1758; Recent, tropical Indo-Pacific.
Synonyms:
Pallium Klein, 1753: 131 [not binomial].
Pallium Martini, 1774: 129 [not binomial].

Pallium Schumacher, 1817: 41, 120 [not of Schröter, 1802; junior synonym of *Pecten* Müller, 1776 (s.l.)]. Type species (by monotypy): *Pallium striatum* Schumacher, 1817 [junior synonym of *Ostrea plica* Linnaeus, 1758]; Recent, Indo-West Pacific.

Decadopecten Swainson, 1840: 388. Type species (by monotype): *Pecten plicata* G.B. Sowerby 2nd, 1839 [error for *Pecten plica* G.B. Sowerby 2nd, 1839, junior synonym of *Ostrea plica* Linnaeus, 1758].

Dentipecten [Rüppell] Gray, 1847: 200. Type species (by original designation): *Ostrea plica* Linnaeus, 1758 [objective; Hertlein, 1969: N365].

Comptopallium Iredale, 1939: 359. Type species (by original designation): *Comptopallium pauciplicatum* Iredale, 1939 [junior synonym of *Ostrea radula* Linnaeus, 1758]; Recent, Queensland, Australia.

Diagnosis: Free swimming member of the Decatopectinini, suborbicular to elongate, laterally compressed; shell with 3-15 rounded radial costae, sculptured with closely arranged commarginal lamellae, anterior and posterior auricles subequal to equal, byssal notch nearly absent, no byssal fasciole, ctenolium weakly developed.

Distribution: Miocene-Recent (Hayami, 1989: 15); Indo-Pacific; littoral to sublittoral depths.

Plate 5.

Figures 20-21. *Laevichlamys superficialis* (Forsskål, 1775). TAU-MO 28533, Bilaiyim Lagoon, H 36.0mm. **20.** rv, exterior. **21.** rv, interior. **22.** *Juxtamusium maldivense* (E.A. Smith, 1903). TAU-MO 28563, off Gesirat Farún, 50m, H 13.5mm, rv, exterior. **23-24.** *Pedum spondyloideum* (Gmelin, 1791). HUJ 30483, Elat, H 108mm, spm. **23.** lv, exterior. **24.** lv, interior. **25.** *Decatopecten amiculum* (Philippi, 1851). ISRSE/0155, Dahlak Archepelago, 18-22m, H 41.5mm, rv, exterior.

Remarks: Hertlein (1969: N365) placed *Decatopecten* in a suprageneric *Decatopecten* group, whereas Waller (1986: 40) and subsequently Vaught (1989: 119) placed it in the new tribe Decatopectinini Waller, 1986 with the type genus *Decatopecten* Rüppel [sic] in G.B. Sowerby 2nd, 1839.

Decatopecten amiculum (Philippi, 1851)
(Plate 5, fig. 25, plate 9, figs. 42-43)

-*Pecten amiculum* Philippi, 1851: 89.
**Pecten flabelloides* Reeve, 1852: spec. 21, pl. 4, figs. 21a, 21b.
**Pecten helleri* Preston, 1909: 139, pl. 22, fig. 15 (Syn. nov.).
Pecten flabelloides.- P. Fischer, 1871: 212; Küster & Kobelt, 1888: 66, pl. 17, fig. 11; Shopland, 1902: 171.
Pecten flabelloides.- Shopland, 1896: 234.
Chlamys (Pallium) amiculum.- Lamy, 1935: 313.
Decatopecten amiculum.- Abbott & Dance, 1982: 307, illustr.; Oliver, 1982: 14; 1992: 77, pl. 12, fig. 9; Bernard, Cai & Morton, 1993: 51.
Decadopecten (Decadopecten) amiculum.- Rombouts, 1991: 36, pl. 13, fig. 7.

Type material: Pecten amiculum Philippi: Not traced in ZMB, or MNHNS (pers. comm. Dr. O.G. Herrera, 25 September 1989); *Pecten flabelloides* Reeve: Lectotype BMNH 1996403/1 herein designated, figured in Reeve (1852: sp. 21, pl. 4, fig. 21a), 2 paralectotypes BMNH 1996403/2-3; *Pecten helleri* Preston: Holotype, BMNH 1915.1.6.47.

Type localities: P. amiculum: "Madagascar" [Malagasy Republic]; *P. flabelloides:* Moluccas [Maluku], Indonesia; *P. helleri:* "Ceylon" [Sri Lanka].

Material examined: The type material. RED SEA: Um Rashrash, 1 v, HUJ 35739. GULF OF ADEN: Djibouti, 4m, among sand and rubble, 1 spm., HD 2131; Djibouti, 20-30m, soft sediments, live, 6 spms., HD 2176; Yemen, off Abyan, 20m, soft substrates, 1 v, HD 2835.

Distribution: Red Sea, Gulf of Aden, east coast of Africa to Natal (South Africa), Persian Gulf, extending eastwards to the Philippines and Indonesia. Littoral to sublittoral depths, living free on soft substrates.

Remarks: The present species differs mainly from the closely related species *Decatopecten plica* (Linnaeus, 1758) by having more weakly developed radial plicae (7-11), which are usually more compressed.

For description of the present species see Rombouts (1991: 36) and Oliver (1992: 77).

Decatopecten plica (Linnaeus, 1758)
(Plate 9, figs. 40-41)

**Ostrea plica* Linnaeus, 1758: 697.
Pecten plicatus Chemnitz, 1784: 292, pl. 62, figs. 598a-b [not binomial].
**Pallium striatum* Schumacher, 1817: 120, pl. 4, figs. 4a-b.

**Pecten subplicatus* G.B. Sowerby 2nd, 1842: 64, pl. 13, fig. 37, pl. 14, figs. 72, 73, 81.
Ostrea plica.- Linnaeus, 1764: 526; 1767: 1145; Gmelin, 1791: 697; Dillwyn, 1817: 252; Wood, 1825: 48, pl. 10, fig. 13; Hanley, 1855: 105; Dodge, 1952: 169.
Pecten plicatus Chemnitz, 1784: 292, pl. 62, figs. 598a-b [not binomial].
---------- Savigny, 1817: pl. 13, fig. 6.
Pecten plica.- Lamarck, 1819: 167; Deshayes, 1836: 136; G.B. Sowerby 2nd, 1842: 65, pl. 20, figs. 237; Chenu, 1843: 5, pl. 16, figs. 9-12; Catlow & Reeve, 1845: 82; Reeve, 1852: spec. 16, pl. 3, fig. 16; Vaillant, 1865: 112; Issel, 1869: 104, 372; Dunker, 1882: 242; Cooke, 1886: 135; Küster & Kobelt, 1888: 53, pl. 14, figs. 3-4; Paetel, 1890: 232; Smith, 1891: 434; Stearns & Pilsbry, 1895: 144; Anthony, 1906: 499; Hall & Standen, 1907: 67; Melvill & Standen, 1907: 809; Melvill, 1909: 127; Ryland, 1951: 22.
Pecten ---------- Audouin, 1828: 208, pl. 13, fig. 6.
Pecten velutinus G.B. Sowerby 2nd.- Issel, 1869: 383.
Pecten (Pallium) plica.- Macandrew, 1870: 449; Hall & Standen, 1907: 67; Lynge, 1909: 60.
Pallium plica.- Smith, 1903: 622; Lamy, 1935: 313.
Chlamys plica.- Pallary, 1926: 121, pl. 17, fig. 6; Kuroda, 1931: 83; Pallary, 1932: 317; Barnard, 1964: 430; Smythe, 1979: 71.
Chlamys (Pallium) plica.- Lamy, 1928: 219; Dautzenberg, 1929: 562; Lamy, 1938: 13; Moazzo, 1939: 32.
Chlamys (Decadopecten) plica.- Cox, 1929: 201, 205; Eames & Cox, 1956: 49.
Decatopecten plica.- Habe, 1951: 78; Kira, 1962: 174, pl. 53, fig. 11; Mastaller, 1979: 142; Bosch & Bosch, 1982: 159, illustr.; Oliver, 1982: 14; 1992: 72, text-figs. 20a-b, 77, pl. 12, figs. 8a-b [references, description]; Bosch, Dance, Moolenbeek & Oliver, 1995: 232, fig. 1008; Dijkstra, 1997: 330, fig. 36.
Decatopecten (Decatopecten) plica.- Hertlein, 1969: 365, figs. C87: 4a-b.
Decatopecten plica.- Habe, 1977: 85; Abbott & Dance, 1982: 307, illustr.; Bernard, Cai & Morton, 1993: 51.
Decadopecten (Decadopecten) plica.- Rombouts, 1991: 37, pl. 13, figs. 8, 8a.
Decatopecten striatus.- Bernard, Cai & Morton, 1993: 51.

Type material: Ostrea plica Linnaeus: Lectotype (designated by Dijkstra, in press) and 2 paralectotypes, LSL [not registered]; one paralectotype and 2 possible paralectotypes, UUZM; *Pallium striatum* Schumacher: 2 syntypes ZMUC [not registered]; *Pecten subplicatus* G.B. Sowerby 2nd: No specimens in the BMNH at London resemble Sowerby's figures or descriptions, therefore type material is not available (J. Pickering and K. Way, pers. comm.).

Type localities: Ostrea plica: 'O. Indico', restricted to Indonesia by Dijkstra [in press]; *Pallium striatum:* Indonesia; on label "Canton"; *Pecten subplicatus:* "Amboina" [Ambon, Maluku, Indonesia].

Material examined: The type material. RED SEA: Suez, 1 v, HUJ 35738; Ras Matarma, beach, 3 v, HD 3354; Aqaba, 1 v, HUJ 35737; off Elat, 2-4m, under stone, sand, 1 spm., HD 173; off Elat, 2-4m, under rock, live, 1 spm., HD 397; off

Hurghada, 20-40m, soft substrates, live, 8 spms., HD 3343; Ras Sudr, 1 v, HUJ 21586; Um Rashrash, 2 v, HUJ 35739; off Ras Sudr, beach, 1 v, 25.x.1971, NS 8581; off Ras-el-Kanisa, 1 spm. (juv.), 28.x.1971, NS 8534; Dahlak Archipelago, 15°17'N, 40°10'E, 18-22m, 1 v, 16.x.1965, ISRSE 0155; Dahlak Archipelago, 15°17'N, 40°10'E, 18-22m, 1 v (juv.), 16.x.1965, ISRSE 0162; Dahlak Archipelago, 15°58'N, 40°19'E, 9-12m, 1 spm., 17.x.1965, ISRSE 2590; Dahlak Archipelago, 27-37m, 1 v, 1 fragment, 19.x.1965, ISRSE 1389; Dahlak Archipelago, 15°35'N, 40°40'E, 20-24m, 1 spm., 22.x.1965, ISRSE 1695a.

Distribution: Red Sea, Gulf of Aden, east coast of Africa to South Africa, Malagasy, Réunion, Mauritius, Arabian Sea, Persian Gulf, extending to southern Japan and southwards to Indonesia. Subtidal to sublittoral depths, living on soft sediments (mud, sand with rubble).

Remarks: This widely distributed species consistently varies in number of radial costae (3-5), thickness, convexity and colour.

D. amiculum (Philippi) is a closely related species having the same distribution. *P. striatum* and *P. subplicatus* are morphologically similar to the type specimen of *O. plica* and come from the same area.

For the description of the present species see Oliver (1992: 77).

Genus **Excellichlamys** Iredale, 1939

Excellichlamys Iredale, 1939: 366.
Type species (by original designation): *Pecten spectabilis* Reeve, 1853; Recent, locality unknown.

Diagnosis: Free-living member of Decatopectinini, orbicular to elongate, laterally compressed, equilateral, right valve more convex than left, with 8-11 radial plicae, sculptured with closely spaced commarginal lamellae, anterior and posterior auricles equal to unequal, byssal notch rather deep, byssal fasciole relatively wide, ctenolium weakly developed.

Distribution: Miocene-Recent (Hayami, 1989: 15); Indo-West Pacific; littoral to sublittoral depths.

Remarks: Hertlein (1969: N366) treated Excellichlamys as a subgenus of *Semipallium* [Jousseaume] Lamy, 1928, placed in the suprageneric group *Decatopecten*. However, Waller (1986: 40) and subsequently Vaught (1989: 119) treated *Excellichlamys* as an extant genus in the tribe Decatopectinini.

Excellichlamys spectabilis (Reeve, 1853)
(Plate 6, figs. 26-27)

**Pecten spectabilis* Reeve, 1853: spec. 128, pl. 29, fig. 128.
Pecten histrionicus (Gmelin) var.- Petit, 1853: 150, pl. 5, fig. 2.
Pecten spectabilis.- Reeve, 1860: 58; Lischke, 1871: 159; Martens, 1880: 314; Küster & Kobelt, 1888: 61, pl. 16, fig. 3; Paetel, 1890: 234; Stearns & Pilsbry, 1895: 14.
Chlamys spectabilis.- Hidalgo, 1904: 380.

Pecten (Aequipecten) histrionicus var. *spectabilis*.- Dautzenberg & Bavay, 1912: 22.
Chlamys (*histrionica* var. ?) *spectabilis*.- Kuroda, 1932: 95.
Aequipecten histrionicus var. *spectabilis*.- Lamy, 1935: 314.
Chlamys histrionicus [sic] var. *spectabilis*.- Viader, 1937: 61.
Excellichlamys spectabilis.- Iredale, 1939: 366; Cotton, 1964: 10; Thornley, 1968: 9; Kira, 1967: 139, pl. 50, fig. 2; Kuroda, Habe & Oyama, 1971: 366, pl. 79, figs. 12-13; Waller, 1972: 224, 225F, 227, 246-250, 247F, 247T, 248T, 258, 259, pl. 5, figs. 87-92, pl. 6, figs. 93-102 [references, description, distribution, ecology]; Abbott & Dance, 1982: 308; Oliver, 1982: 15; Bernard, Cai & Morton, 1993: 51 [distribution]; Mühlhäusser, 1985: 9; Dijkstra, 1987a: 9, illustr.; 1991b: 44 [references]; 1997: 327, figs. 24-27; Oliver, 1992: 72, 77, pl. 14, figs. 1a-b, text-figs. 22a-b.
Excellichlamys cf. *spectabilis*.- Sharabati, 1984: pl. 44, figs. 6-6a.

Type material: Holotype UMZC 1461.

Type locality: Unknown.

Material examined: The type material. RED SEA: Elat, 1 spm., 1 v, MO 28534; Elat, 3 v, HUJ 21581; Elat, 1 spm. + 5 v, HUJ 35730; Elat, 4-8m, among coral rubble, live, 1 spm., HD 177; S of Elat, 6-8m, among coral rubble, live, 1 spm., HD 398; 20km S of Elat, 10-15m, amongst coral, live, 2 spms., HD 3021; Aqaba, 2 v, HUJ 35731; Aqaba, 3 v, HUJ 35732.

Distribution: Red Sea, east coast of Africa to South Africa, Réunion, Mauritius, extending eastwards to southern Japan and New Caledonia. Subtidal to sublittoral depths, living byssally attached under rocks or corals or amongst coral rubble on sand.

Remarks: Present material from the Red Sea is variable in radial costae (3-5 prominent radial costae with lower intercostal ribs, which are also variable in number). In some specimens the left valve is more convex than in the type material, and compressed near the ventral margin. The auricles are very unequal, but not as strongly as in Polynesian material.

Excellichlamys xishaensis (Wang, 1985) from the tropical western Pacific is morphologically similar to Polynesian specimens, known as *Excellichlamys parva* (G.B. Sowerby 1st, 1835), which name is preoccupied by Da Costa (1778). *E. xishaensis* differs from the present species in its strongly unequal auricles and fewer primary radial costae.

For description of the present species see Waller (1972: 247).

Genus **Glorichlamys** Dijkstra, 1991

Glorichlamys Dijkstra, 1991b: 45.
Type species (by original designation): *Pecten elegantissimus* Deshayes, 1863; Recent, Réunion. For diagnosis and comparison see Dijkstra (1991b: 45).

Distribution: Recent; Indo-West Pacifc; littoral to sublittoral depths.

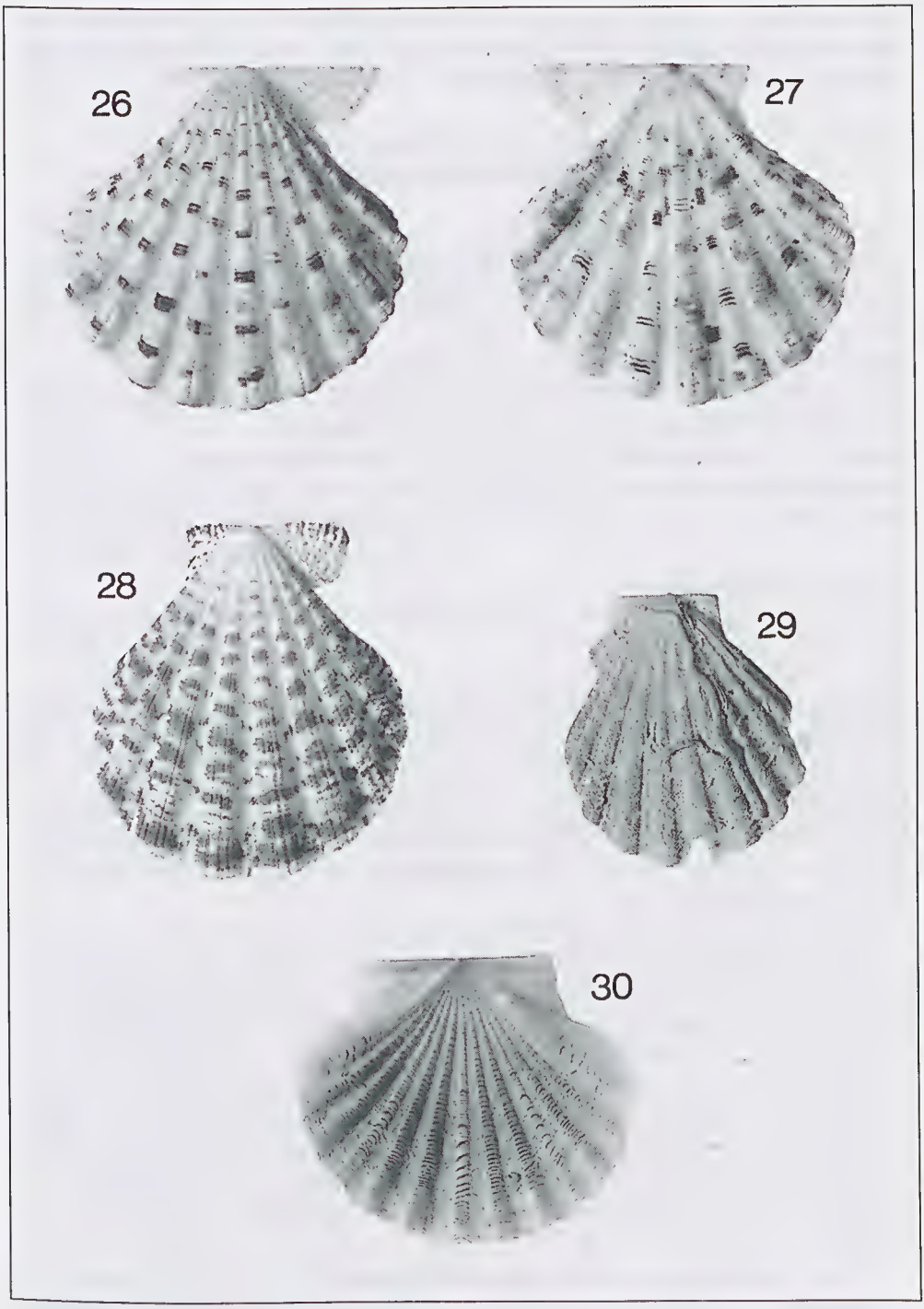


Plate 6.

Figures 26-27. *Excellichlamys spectabilis* (Reeve, 1853). TAU-MO 28534, Elat, H 26.0mm, spm. **26.** rv, exterior. **27.** lv, exterior. **28.** *Gloripallium maculosum* (Forsskąl, 1775). ZMUC, Elat, H 51.9mm, rv, exterior. **29.** *Semipallium crouchi* (E.A. Smith, 1892). TAU, off Mersat Abu Samra, 132-137m, H 12.6mm, lv, exterior. **30.** *Pecten erythraeensis* G.B. Sowerby 2nd, 1842. TAU-NS 16466, off Ras Abu Rudeis, 42-46m, H 40.9mm, lv, exterior.

Remarks: Glorichlamys was placed by Dijkstra (1991b: 45) in the tribe Decatopectinini Waller, 1986, and compared with *Gloripallium* Iredale, 1939, *Excellichlamys* Iredale, 1939, and *Bractechlamys* Iredale, 1939.

Glorichlamys quadrilirata (Lischke, 1870)
(Plate 10, figs. 46-47)

-*Pecten quadriliratus* Lischke, 1870: 29.
Pecten quadriliratus.- Lischke, 1871: 158, pl. 9, figs. 5-6; Dunker, 1882: 240; Küster & Kobelt, 1888: 136, pl. 37, figs. 6-7; Paetel, 1890: 233; Pilsbry, 1895: 144; Bavay, 1905: 29; Yokoyama, 1924: 57, pl. 4, fig. 10.
Pecten (Chlamys) quadriliratus.- Dautzenberg & Bavay, 1912: 4.
Chlamys quadrilirata.- Kuroda, 1932: 93; Lamy, 1935: 4; Kira, 1967: 136, pl. 49, fig. 6; Dijkstra, 1989: 12, 13, 14, illustr.; 1990: 4, 5, illustr.
Chlamys (Chlamys) quadrilirata.- Habe, 1951: 74; Azuma, 1960: 75.
Bractechlamys quadrilirata.- Habe, 1977: 83; Wang, 1983c: 531, 533, pl. 1, figs. 8-10.
Glorichlamys quadrilirata.- Dijkstra, 1991b: 45; 1993: 10, illustr.

Type material: Untraceable.

Type locality: Nagasaki, Japan.

Material examined: RED SEA: Elat, 20-25m, under rock, sand and rubble, 1 spm., HD 2879.

Distribution: Red Sea, Malagasy, Thailand, extending eastwards to southern Japan, China, Philippines, Indonesia, Australia, New Caledonia, and Fiji Islands. Littoral to sublittoral depths, living under rocks, coral boulders or among coral rubble on soft substrates.

Description: Shell small, up to ca. 25mm high, suborbicular to elongate, inequivalve, slightly inequilateral, both valves convex and radiated, inside plicated, auricles strongly unequal, umbonal angle ca. 85-90°, auricular crura well developed, resilium triangularly oblong.

Left valve sculptured with 8-11 prominent quadripartite (in mature individuals) rounded radial costae and 1-3 interstitial radial riblets. Microsculpture with closely arranged commarginal lamellae. Anterior auricle with 10-12 weakly and strongly developed radial riblets, lamellated and noduliferous on dorsal margin, posterior auricle very small with few fine radial riblets.

Right valve with broad prominent quadripartite radial costae, less rounded than of those of the left valve, one interstitial radial riblet per interval. Microsculpture as in left valve. Anterior auricle with ca. 10 squamose radial riblets. Byssal notch weak, byssal fasciole small, active ctenolium with 4-6 teeth on the suture.

Colour of left valve cream with purple or brown maculations, right valve paler or whitish.

Remarks: This is a new record for the Red Sea. Only one dead specimen has been collected so far, which is morphologically similar to the original description of Lischke. For conchological comparison with *Glorichlamys elegantissima* see Dijkstra (1989: 12-15).

Genus **Gloripallium** Iredale, 1939

Gloripallium Iredale, 1939: 357.
Type species (by original designation): *Ostrea pallium* Linnaeus, 1758; Recent, "O. Australiore et Indico" [restricted to Ambon, Maluku, Indonesia by Dijkstra (in press)].

Diagnosis: Free-swimming Decatopectinini, suborbicular to elongate, solid, slightly equiconvex, equilateral to somewhat oblique, with 7-15 regularly developed primary radial plicae, secondary radial riblets, commarginal lamellae, antimarginal microsculpture in early growth-stage, no shagreen microsculpture, auricles unequal, byssal notch moderately deep, byssal fasciole rather small, ctenolium well developed.

Distribution: Miocene-Recent (Hayami, 1989: 15); Indo-West Pacific; littoral to sublittoral depths.

Remarks: Hertlein (1969: N357) treated *Gloripallium* as a synonym of *Cryptopecten* Dall, Bartsch & Rehder, 1938. Waller (1986: 40) and subsequently Vaught (1989: 119) interpreted *Gloripallium* as an extant genus in Decatopectinini.

Gloripallium maculosum (Forsskål, 1775)
(Plate 6, fig. 28)

**Ostrea maculosa* Forsskål, 1775: 26, no. 59; 123, no. 59 [Original diagnosis].
'Pallium variegatum et aculeatum' Chemnitz, 1784: 305, pl. 64 fig. 608 [invalid publication].
Ostrea sanguinolenta Gmelin, 1791: 3322, no. 41.
-*Pecten pictus* Deshayes *in* Laborde & Linant, 1830: 66, figs. 1, 2.
**Pecten concinnus* Reeve, 1853: spec. 167, pl. 35, fig. 167.
-*Pecten luxurians* Küster *in* Küster & Kobelt, 1859: 111, no. 70, pl. 32, fig. 1.
Ostrea sanguinolenta.- Dillwyn, 1817: 253, no. 15; Wood, 1825: 49, no. 16.
---------- Savigny, 1817: pl. 13, fig. 8.
Pecten sanguinolentus.- Bosc, 1824: 262; G.B. Sowerby 2nd, 1842: 73, no. 86, pl. 13, fig. 59; Hanley, 1843: 283; Catlow & Reeve, 1845: 83, no. 83; Reeve, 1853: sp. 98, pl. 24, fig. 89 [sic] [fig. 98]; Reeve, 1860: 58, no. 127; Vaillant, 1865: 112, no. 39; Issel, 1869: 102, 372; Macandrew, 1870: 449; P. Fischer, 1870: 168; Cooke, 1886: 134; Küster & Kobelt, 1888: 40, no. 9, pl. 11, fig. 2; Paetel, 1890: 233; Smith, 1891: 390; Shopland, 1896: 234; 1902: 171.
Pecten ---------- Audouin, 1828: 208, pl. 13, fig. 8.
Pecten concinnus.- Issel, 1869: 103; Macandrew, 1870: 449; Martens *in* Möbius, 1880: 314; Cooke, 1886: 134; Paetel, 1890: 229.

Pecten luxurians.- Paetel, 1890: 231.
Chlamys sanguinolenta.- Pallary, 1926: 122, pl. 17, fig. 8; Lamy, 1928: 169; 1938: 12 [in part]; Cox, 1929: 206, no. 7; Pallary, 1932: 317; Moazza, 1939: 31; Dance, 1974: 234, illustr.; Mastaller, 1978: 138; 1979: 141.
Pecten pictus.- Tomlin & Salisbury, 1928: 33.
Chlamys concinna.- Cox, 1929: 204.
Chlamys luxurians.- Cox, 1929: 205.
Chlamys picta.- Cox, 1929: 205.
Manupecten sanguinolentus.- Lamy, 1935: 312; Franc, 1956: 54.
Chlamys (Pallium) sanguinolenta.- Moazzo, 1939: 31.
Chlamys (Aequipecten) sanguinolenta.- Eames & Cox, 1956: 44.
Excellichlamys concinna.- Waller, 1972: 248, 250, figs. 107-110.
Aequipecten sanguinolentus.- Selli, 1973: 183. [references]
Chlamys sanguinolenta.- Dance, 1974: 234, illustr.; Mastaller, 1987: 210.
Cryptopecten sanguinolentus.- Oliver, 1982: 11.
Excellichlamys sanguinolenta.- Abbott & Dance, 1982: 308, illustr.
Gloripallium sanguinolentum.- Sharabati, 1984: pl. 44, figs. 9, 9a-c; Rombouts, 1991: 43, pl. 15, figs. 5, 5a.
Ostrea maculosa.- Yaron, Schiøtte and Wium-Andersen, 1986: 181, figs. 21, 22.
Chlamys (Cryptopecten) maculosa.- Oliver, 1992: 72, 76, pl. 14, fig. 2, text-figs. 23a-b.

Type material: Ostrea maculosa Forsskål: Lectotype designated and figured by Yaron, Schiøtte & Wium-Andersen (1986: 181, fig. 22) ZMUC BIV-29, 2 paralectotypes (lv + rv) ZMUC BIV-306; *Ostrea sanguinolenta* Gmelin: Junior objective synonym of *O. maculosa; Pecten pictus* Deshayes *in* Laborde & Linant: Type material untraceable; *Pecten concinnus* Reeve: 2 syntypes BMNH 40.4.6.52.1-2; *Pecten luxurians* Küster: Type material untraceable [pers. comm. Dr. R. Zilch].

Type localities: = *Ostrea maculosa* : Red Sea, Gulf of Suez, Suez; *Ostrea sanguinolenta:* "mari rubro" [Red Sea]; *Pecten pictus:* Red Sea; *Pecten concinnus:* Red Sea; *Pecten luxurians:* Red Sea.

Material examined: The type material. RED SEA: Elat, 1 spm., HUJ 35733; Elat, 2 v, HUJ 35734; Elat, 7 v, HUJ 35736; Elat, 4-6m, amongst coral, live, 1 spm., HD 439; Elat, 4-10m, amongst coral, live, 5 spms. (juv.), HD 1516; Elat, 9-12m, under coral, 1 spm., HD 2627; Elat, 8-9m, outside of reef, on coral, live, 1 spm., HD 2629; Aqaba, 1 spm., HUJ 35735; 30km S of Elat, 6-10m, amongst coral, live, 1 spm., HD 914 [figured in Rombouts (1991: pl. 15 fig. 5)]; Nabeck, 4-6m, amongst coral, live, 3 spms. (juv.), HD 1353; Elat, 5 spms., 1 v, 1964/65, leg. M. Blom, ZMUC; Ras Burqa, beach, 1 spm., 6.X.1968, NS 4481; Ras Burqa, beach, 1 spm., 6.X.1968, NS 4483; Ras Burqa, 8-10m, 1 v, HUJ 35651. GULF OF ADEN: Djibouti, Tadjourah Gulf, 20m, sand and coral rubble, live and dead, 2 spms. + 3 v, HD 3691.

Distribution: Red Sea and Gulf of Aden. Littoral to sublittoral depths, living amongst coral and coral rubble on sandy substrates.

Remarks: All authors overlooked Forsskål's description of *O. maculosa* from the Red Sea, prior to Yaron *et al.* (1986), and mostly used Gmelin's name *O. sanguinolenta;* Gmelin only cited Chemnitz (1784). Chemnitz also overlooked Forsskål's publication, but mentioned Forsskål and Niebuhr's expedition to the Red Sea in his description: *"Sie ist von der gelehrten Gesellschaft, welche unser höchstseliger König nach Arabien gesandt, hierher geschicket worden."* [The species is from the scientific expedition, which was sent to Arabia by our honourable king]. Thus Gmelin indirectly referred to the material described by Forsskål (1775).

P. pictus Deshayes *in* Laborde & Linant is preoccupied by Da Costa (1778: 144) and the type material is morphologically similar to *O. maculosa.*

P. concinnus Reeve is preoccupied by Koch & Dunker (1837: 42) [not Philippi, 1845] and the type material is identical to young specimens of *O. maculosa.*

P. luxurians Küster is also similar to *O. maculosa* and Küster also mentioned in the original description the close alliance of *O. sanguinolenta.* Cox (1929: 205) treated *P. luxurians* as a variation of *O. sanguinolenta.*

For description of the present species see Oliver (1992: 76).

Gloripallium pallium (Linnaeus, 1758)
(Plate 10, figs. 48-49)

**Ostrea pallium* Linnaeus, 1758: 697, no. 163.
-*Pecten novaeguineae* Tenison Woods, 1878: 267.
Pecten pallium.- Lamarck, 1819: 170; Reeve, 1853: spec. 63, pl. 17, figs. 63a-c; Küster & Kobelt, 1888: 39, 103, pl. 11, figs. 1, 5, pl. 28, figs. 7-8, pl. 29, fig. 1.
Pecten (Aequipecten) pallium.- Dautzenberg & Bavay, 1912: 19; Adam & Leloup, 1939: 59.
Gloripallium pallium.- Iredale, 1939: 357; Kira, 1972: 140, pl. 50, fig. 10; Waller, 1972: 239, pl. 3, figs. 45-47 [description, ecology, distribution]; Dijkstra, 1984c: 17, illustr.; 1991b: 46; 1997: 316, 328, figs. 28-32; Mastaller, 1979: 140; 1987: 210; Rombouts,1991: 42, pl. 15, figs. 4, 4a.
Chlamys (Cryptopecten) pallium.- Hertlein, 1969: N357, fig. C79: 1c.

Type material: Ostrea pallium Linnaeus: Lectotype (H 42 mm, L 41mm) LSL [not registered] designated by Dijkstra [in press], 3 paralectotypes LSL, 2 possible paralectotypes UUZM [not registered]; *Pecten novaeguineae* Tenison Woods: Holotype not traced in Tasmanian Museum and Art Gallery at Hobart [Kemp, pers. comm.].

Type localities: Ostrea pallium: "O. australiore and Indico". More restricted by Dijkstra [in press] to the Moluccas [Maluku], Indonesia; *Pecten novaeguineae:* Pleistocene, Hall Sound, Papua New Guinea.

Material examined: The type material. RED SEA: Elat, 2-4m, among coral rubble, live, 1 spm., HD 178; Elat, 4-6m, among coral rubble, 1 spm., HD 400; Assab, 2-4m, among coral rubble, live, 2 spms., HD 172; SOMALIA: off Mogadiscio, 15-20m, soft substrates, live, 1 spm., HD 2966; off Mogadiscio, 20-25m, amongst rubble, sand, live, 1 spm., HD 6483.

Distribution: Red Sea, Gulf of Aden, east coast of Africa to South Africa, Malagasy, Réunion, Mauritius, Arabian Sea, extending eastwards to southern Japan to the central Pacific; not living in the Hawaiian Islands. Intertidal to littoral depths, living byssally attached to rocks, stones, corals or amongst coral rubble on soft substrates.

Remarks: Although *G. pallium* is a very common pectinid species with a wide distribution in the Indo-Pacific, it seems to be rare in the Red Sea. This is the first record of living specimens from that region. Material examined is morphologically similar to the type specimens.

For description of the present species see Waller (1972: 239).

Genus **Juxtamusium** Iredale, 1939

Juxtamusium Iredale, 1939: 368.
Type species (by original designation): *Juxtamusium oblectatum* Iredale, 1939 [junior synonym of *Pecten (Chlamys) coudeini* Bavay, 1903].

Diagnosis: Free-living Decatopectinini, thin, compressed, suborbicular, equilateral, auricles unequal, with numerous irregularly to more regularly spaced radial riblets with microscopic overrunning commarginal lamellae, hinge plate flat, lacking prominent crura, grooves or denticles, resilial insertion fold on anterior auricle only, resilifer obliquely oblong, byssal fasciole narrow, byssal notch shallow, ctenolium present on suture of both valves.

Distribution: Pliocene - Recent (Waller, 1972: 253); Indo-West Pacific; littoral to sublittoral depths.

Remarks: Hertlein (1969: N357) treated *Juxtamusium* as a subgenus of *Chlamys* in the suprageneric group of *Chlamys*. Waller (1986: 40) and subsequently Vaught (1989: 119) considered *Juxtamusium* to be an extant genus of Decatopectinini.

Juxtamusium is the only known genus of pectinids with a ctenolium on the left valve as well as the right (Waller, 1984: 211).

Juxtamusium maldivense (Smith, 1903)
(Plate 5, fig. 22)

**Pecten maldivensis* Smith, 1903: 622, pl. 36, figs. 19-20.
Pecten maldivensis.- Melvill & Standen, 1907: 809; Melvill, 1909: 126; Dautzenberg & Bavay, 1912: 17; Iredale, 1939: 368.
Chlamys maldivensis.- Lamy, 1935: 311; Viader, 1937: 61; Oliver, 1982: 10.
Juxtamusium maldivense.- Waller, 1972: 224, 226F, 227, 250-254, 251F, 252T, 258, 259, pl. 7, figs. 111-127, pl. 8, fig. 134; Thayer, 1975: 447-449, 3 figs.; Abbott & Dance, 1982: 315, illustr.; Dijkstra, 1984b: 8, illustr.; Sharabati, 1984: pl. 44, figs. 4-4a; Waller, 1984: 211.
Chlamys (Juxtamusium) maldivensis.- Oliver, 1992: 71, 76, pl. 12, figs. 5a-b, text-figs. 10a-b.

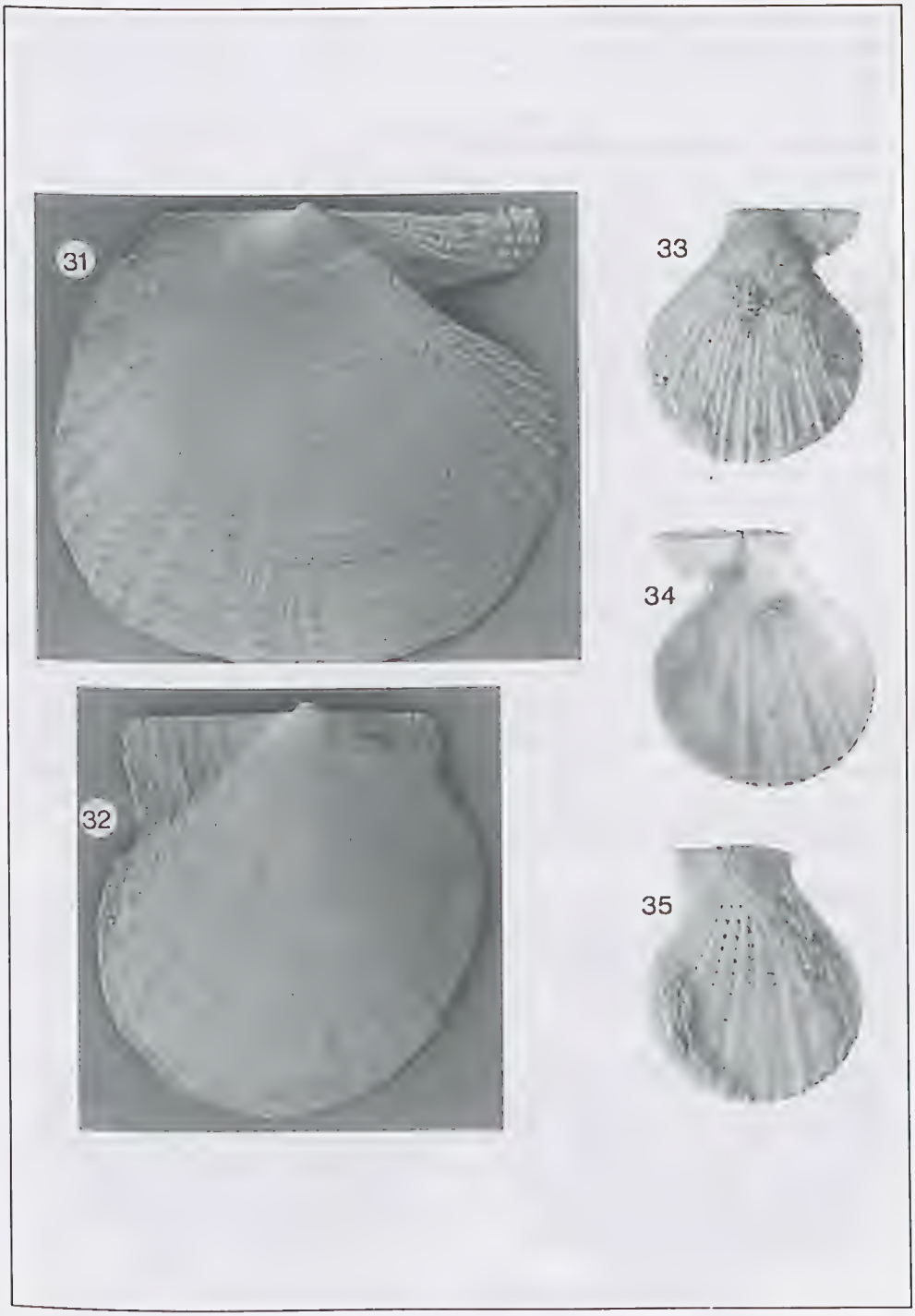


Plate 7.

Figures 31-32. *Delectopecten musorstomi* Poutiers, 1981. **31.** TAU-MO 28555, Elat, opp. Old Port, 121m, H 4.7mm, rv, exterior. **32.** TAU-MO 28556, Elat, opp. Oil Port, 344m, H 4.0mm, lv, exterior. **33-35.** *Laevichlamys rubromaculata* (G.B. Sowerby 2nd, 1842). ZMUC, Elat, H 29.9mm, spm. **33.** rv, exterior. **34.** rv, interior. **35.** lv, interior.

Type material: Lectotype [second largest specimen] designated and refigured by Waller (1972: 250, figs. 111-112) BMNH 1903.9.17.49, 4 paralectotypes BMNH 1903.9.17.50-53. Largest specimen measured by Smith, was not figured by him.

Type locality: Indian Ocean, Maldive Islands, 1-44 fathoms [= 2-80m].

Material examined: RED SEA: off Elat, 40-50m, 1 v, 5.ix.1966, MO 28559; off Elat, 40-50m, 29 v, 5.ix.1966, MO 28581; off Elat, 60-90m, 1 v, 5.ix.1966, MO 28562; off Elat, 40-50m, 2 v, 6.ix.1966, MO 28558; off Elat, 60m, 13 v, 6.ix.1966, MO 28560; off Elat, 40-50m, 21 v, 6.ix.1966, MO 28568; off Elat, 60-80m, 10 v, 7.ix.1966, MO 28564; off Elat, 62-80m, 15 v, 7.ix.1966, MO 28569; off Ras Taba, 55-90m, 1 v (fragment), 14.xii.1967, MO 28576; El Hamira Bay, 15m, 1 v, 14.xii.1967, MO 28566; El Hamira Bay, 47m, 3 v, 14.xii.1967, MO 28570; El Hamira Bay, 24m, 3 v, 14.xii.1967, MO 28567; El Hamira Bay, 24m, 2 v (juv.), 14.xii.1967, MO 28571; off Gesirat Farun, 50m, 3 v, 21.viii.1968, MO 28563; off Gesirat Farun, 50m, 4 v, 21.viii.1968, MO 28573; Elat, opposite Old Port, 121m, 1 v, 10.ix.1968, MO 28575; off Mersat Abu Samra, 46-49m, 12 v, 6.x.1969, MO 28561; off Mersat Abu Samra, 49-55m, 7 v, 6.x.1969, MO 28565; off Mersat Abu Samra, 60m, 3 v, 6.x.1969, MO 28572; off Mersat Abu Samra, 51-53m, 6 v, 6.x.1969, MO 28574; off Wadi Murach, 73-82m, 7 spms., 9.x.1969, NS 16 470; Elat, intertidal, 2 v, xii.1970, NS 7075; Elat, 1 spm., HUJ 35587; Elat, harbour, 1 spm., HUJ 35589; Gulf of Aqaba, 1 v, HUJ 35592; Elat, harbour, 2 v, HUJ 35606; off Elat, 6-10m, under rocks, live, 2 spms., HD 1581; off Elat, 12-14m, on coral, sand, live, 1 spm., HD 2695; off Elat, 8-10m, amongst coral, live, 1 spm., HD 2700 [figured in Rombouts (1991: pl. 26 fig. 7)]; off Elat, 9m, under dead coral, sand, live, 2 spms., HD 2701; off Elat, 6-8m, amongst coral rubble, sand, 1 spm., HD 2702.

Distribution: Red Sea, east coast of Africa to South Africa, Arabian Sea, eastwards to southern Japan, Philippines, Indonesia, and New Caledonia. Littoral to sublittoral depths, living byssally attached to corals and coral rubble on sandy substrates.

Remarks: Specimens from the Red Sea have more prominent sculpture on both valves than those of the type material. *J. coudeini* is closely related, and differs from *J. maldivense* in having a smoother surface with regularly spaced undulating radial costae. Both species are variable in sculpture.

For description and more information on infraspecific variation, functional morphology and ecology see Waller (1972: 252-253).

Genus **Mirapecten** Dall, Bartsch & Rehder, 1938

Mirapecten Dall, Bartsch & Rehder, 1938: 84.
Type species (by original designation): *Mirapecten thaanumi* Dall, Bartsch & Rehder, 1938 [junior synonym of *Pecten mirificus* Reeve, 1853]; Recent, Hawaiian Islands.

Diagnosis: Free-living Decatopectinini, compressed; right valve slightly more convex than left valve, orbicular to suborbicular, inequivalve, inequilateral to equilateral; auricles unequal, microsculpture of closely spaced commarginal lamellae; regularly arranged primary squamous lirae (5-7) to irregularly arranged primary and secondary lirae (7-11), usually squamous, sometimes noduliferous or smooth; byssal notch moderately deep, byssal fasciole rather small, ctenolium well developed.

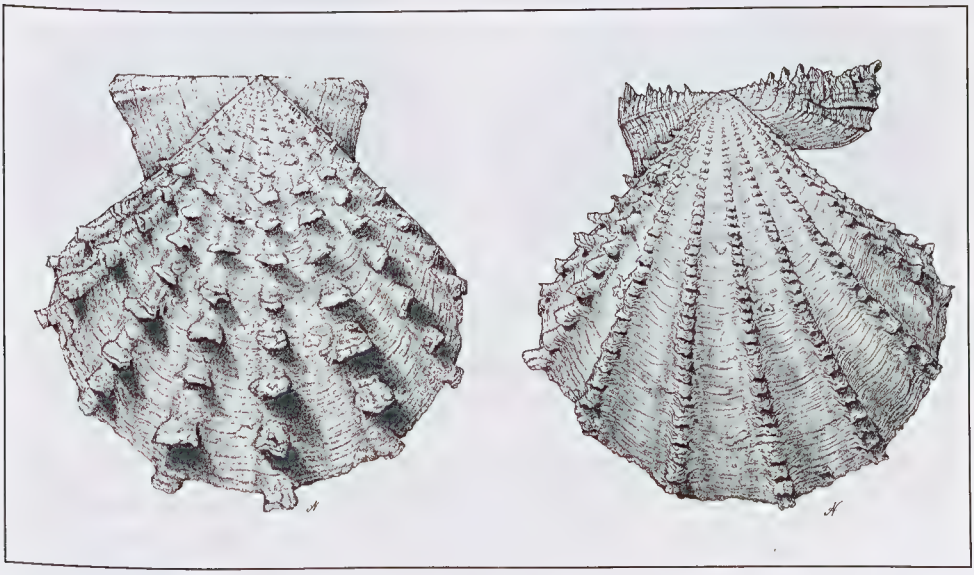
Distribution: Miocene - Recent (Hayami, 1989: 16); tropical Indo-Pacific; littoral to sublittoral depths.

Remarks: Hertlein (1969: N 366) treated *Mirapecten* as a subgenus of *Semipallium* [Jousseaume] Lamy, 1928 and placed it in the supragèneric group of *Decatopecten*. Waller (1986: 40) and Vaught (1989: 119) considered *Mirapecten* to be an extant genus in the tribe Decatopectinini.

Mirapecten yaroni sp. nov.
(Plate 8, figs. 36-39, text-figs. A-B)

Mirapecten rastellum (Lamarck).- Sharabati, 1984: pl. 44, figs. 1, 1a-g [not *Pecten rastellum* Lamarck, 1819].

Description: Shell medium of size to approximately 70mm, convex, inequivalve, subequilateral, orbicular (immature) to slightly elongate (mature), auricles inequal in size, umbonal angle ca. 90°.



Text-figures.
Figures A-B. *Mirapecten yaroni* n. sp. Holotype, ZMUC-BIV 323, Elat, spm. **A.** lv, exterior. **B.** rv, exterior.

Left valve sculptured with 6 regularly arranged radial plicae bearing widely spaced, prominent scales, and a small radial rib near the anterior and posterior margins, interstices with microscopic close-set commarginal lamellae, inconspicuous in early growth stages and more prominent in late growth stages near ventral margin, also produced on plicae. Auricles also with microscopic close-set commarginal lamellae and weak radial riblets (one on anterior, 4 on posterior), on antero- and postero-dorsal margins strongly developed scales.

Right valve with 5 regularly arranged radial plicae with weaker and more closely arranged scales than on left valve, two radial riblets on each side, interstices broader than lirae, interstitial microsculpture similar to that on left valve. Auricles with similar commarginal microsculpture to that on left valve, with 4 radial ribs on anterior, 2 on posterior auricle (much weaker), strongly developed scales on antero- and postero-dorsal margins.

Hinge line straight, byssal fasciole broad, byssal gape rather shallow, active ctenolium with 6 teeth, auricular crura well developed, resilium triangular elongate, weak auricular ridges near anterior and posterior margins. Inner surface plicated with small radial ridges.

Colour pale red with dark red maculations on left valve, much paler on right valve, exterior pigmentation translucent, interior red near ligament and ventral margin, yellowish near auricular margins.

Type material: Holotype (H 43.8mm, L 44.3mm, D 12.0mm) ZMUC BIV-323 , 45 paratypes (34 HD, 6 HUJ, 1 NS, 1 ZMTAU, 3 ZMUC).
RED SEA: Elat, opposite Old Port, 121 m, 1 v (paratype), 10.ix.1968, MO 28536; Tiran, 68m, 1 spm. (juv.) (paratype), 17.x.1969, NS 16 473; Elat, 3 spms. (paratypes), 1964/65, leg. M. Blom, ZMUC; Elat, 3 v (paratypes), HUJ 35744; Aqaba, 3 v, HUJ 35743; off Elat, 10m, amongst dead coral, live, 1 spm. (paratype), HD 180; off Elat, 6-10m, amongst corals, sand, live, 3 spms. (paratypes), HD 427; off Elat, 6-10m, attached to corals, live, 3 spms. (paratypes), HD 915; off Elat, 4-15m, attached to corals, sand, live, 5 spms. (paratypes), HD 1583 [figured in Rombouts (1991: pl. 12 fig. 4b)]; off Elat, 6-10m, amongst coral rubble, sand, live, 3 juvenile spms. (paratypes), HD 2857; off Elat, 6-12m, among corals, live, 9 spms. (paratypes), HD 3690; Elat, 2-5m, amongst coral rubble on sand, 10 spms. (paratypes), HD 6745.

Type locality: Israel, Gulf of Aqaba, Elat.

Distribution: Red Sea. Littoral to sublittoral depths, living on the underside of coral boulders or amongst coral rubble on sandy bottoms.

Discussion: Mirapecten yaroni is morphologically closely similar to the Indo-West Pacific species *Mirapecten rastellum* (Lamarck, 1819) (Dijkstra, 1994: 474). *M. yaroni* grows larger (up to ca. 70mm high, *M. rastellum* ca. 45mm). The regularly arranged radial lirae of both species are identical, although the sculpture on the lirae is different. Strongly developed lamellae are produced in mature specimens of *M. yaroni*, these are nearly absent or weakly spinose on *M. rastellum*. Radial riblets present on the auricles of *M. yaroni* are absent on *M.*

rastellum. The colour of the present species is darker with red and brown spots, whereas *M. rastellum* is paler with more cream colouration. The bathymetric range of both species is also different: *M. yaroni* lives in shallow waters, whereas *M. rastellum* lives in deeper waters.

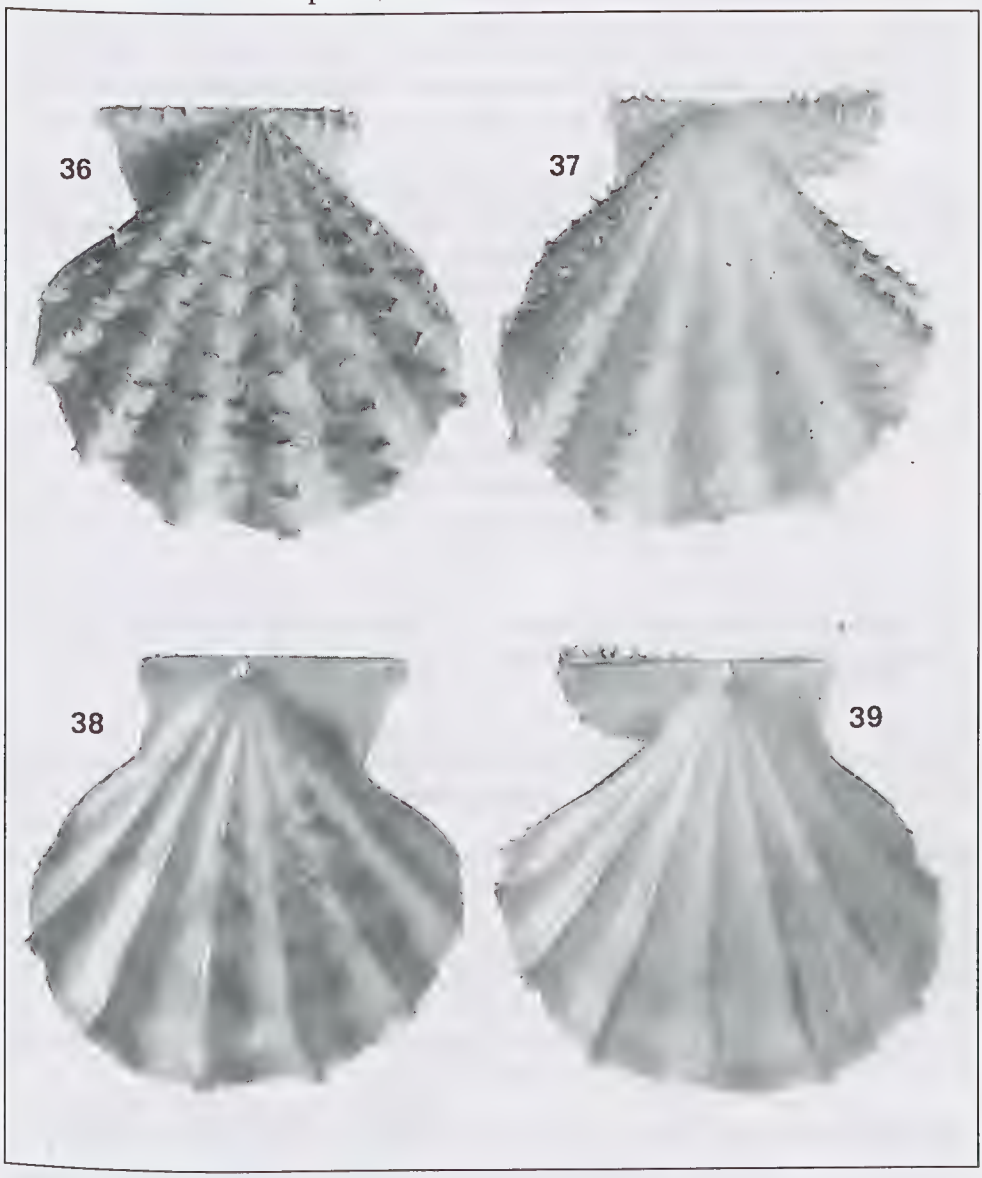


Plate 8.
Figures 36-39. *Mirapecten yaroni* n. sp. Holotype, ZMUC-BIV 323, Elat, H 43.8mm, spm. **36.** lv, exterior. **37.** rv, exterior. **38.** lv, interior. **39.** rv, interior.

Mirapecten moluccensis Dijkstra, 1988, also known from the Indo-West Pacific, differs from *M. yaroni* in its nodulose lirae, more numerous radial riblets on the auricles, and in colour (whitish, with black and reddish linear spots on the left valve).

Mirapecten mirificus (Reeve, 1853), also known from the Indo-West Pacific with a distribution similar to that of *M. rastellum* and a wider distribution than *M. moluccensis*, is strongly inequivalve and inequilateral, with a nearly flat left valve and irregularly developed radial lirae.

Etymology: This species is dedicated to the late Dr. Isaac Yaron (1934-1985), who for many years studied the Red Sea molluscan fauna, and tragically lost his life on April 11th 1985 while diving in the the Gulf of Aqaba.

Remarks: Oliver (1992: 77, pl. 12, figs. 6a-b) erroneously described and figured specimens he called *M. rastellum* from the Gulf of Suez and Jeddah, Red Sea. These are in fact an undescribed *Mirapecten* species. This species will be discussed elsewhere by Dijkstra & Kilburn [in prep.].

Cahill (1979: 36, fig. 6) and Dijkstra (1994: 475) mentioned a new subspecies of *M. rastellum* from the Red Sea, herein described as *M. yaroni*. For other remarks on *Mirapecten* species, see in Dijkstra (1988a, 1991a, 1991b, 1994).

Subfamily **PECTININAE** Wilkes, 1810
Tribe **PECTININI** Wilkes, 1810
Genus **Pecten** Müller, 1776

Pecten Müller, 1776: 31, 248.
Type species (subsequent designation by Schmidt, 1818): *Ostrea maxima* Linnaeus, 1758; Recent, eastern Atlantic.

Synonyms:
Deperetia von Teppner, 1922: 87, 259. Type species (by original designation): *Pecten cristatocostatus* Sacco, 1897; Miocene, Turin, Italy.

Heritschia von Teppner, 1922: 87, 264. Type species (by original designation): *Pecten aduncus* von Eichwald, 1830; Miocene, NW Ukraine.

Jaworskia von Teppner, 1922: 87, 266. Type species (by original designation): *Pecten grandis* J. de C. Sowerby, 1828; Pliocene, Suffolk Crag, England.

Notovola Finlay, 1926: 451. Type species (by original designation): *Pecten novaezelandiae* Reeve, 1852; Recent, New Zealand.

Diagnosis: Free-living Pectinini; shell solid, orbicular to suborbicular, left valve concave to flat, right valve strongly convex, strongly inequivalve, equilateral to subequilateral, auricles equal, with prominent angular to rounded radial ribs, sometimes bifid, microsculpture of closely spaced commarginal lamellae, sometimes absent, cardinal crura well developed, byssal sinus small, no active ctenolium in adult.

Distribution: Miocene - Recent (Waller, 1991: 40); eastern Atlantic, Indo-West Pacific; subtidal to sublittoral depths.

Remarks: For further phylogenetic notes see Fleming (1957) and Waller (1991: 36).

Pecten erythraeensis G.B. Sowerby 2nd, 1842
(Plate 6, fig. 30)

**Pecten erythraeensis* G.B. Sowerby 2nd, 1842: 49, pl. 18, figs. 163-164.
Ostrea ziczac Linnaeus.- Forsskål, 1775: 32, no. 43 [not *Ostrea ziczac* Linnaeus, 1758].
Pecten maximus (Linnaeus) var.- Chemnitz, 1784: 272, pl. 60, figs. 586-587 [not binomial].
---------- Savigny, 1817: pl. 13, fig. 9.
Pecten ---------- Audouin, 1828: 208, pl. 13, fig. 9.
Pecten erythraeensis.- Catlow & Reeve, 1845: 80; Issel, 1869: 103; Macandrew, 1870: 449; Cooke, 1886: 135; Smith, 1891: 434; Tillier & Bavay, 1905: 178; Pallary, 1926: 122, pl. 17, figs. 9.1-4; Lamy, 1928: 219; 1935: 318; 1938: 13; Cox, 1929: 185, 203; Moazzo, 1939: 35; Ryland, 1951: 16; Barash & Danin, 1972: 361; Mastaller, 1979: 140; Oliver, 1982: 15; 1992: 70, 78, pl. 12, figs. 7a-b, text-fig. 8; Kilburn & Dijkstra, 1995: 271, 277.
Pecten medius Lamarck.- P. Fischer, 1865: 244; Vaillant, 1865: 111; Issel, 1869: 260; 373; Küster & Kobelt, 1888: 45, pl. 12, figs. 2-3 [not *Pecten medius* Lamarck, 1819].
Pecten ziczac.- Issel, 1869: 103 [not *Ostrea ziczac* Linnaeus, 1758].
Pecten (Vola) medius.- Issel, 1869: 104 [not *Pecten medius* Lamarck, 1819].
Vola erythraeensis.- Macandrew, 1870: 449; Paetel, 1890: 235.
Pecten filosus Reeve.- P. Fischer, 1870: 168.
Vola filosa.- Sturany, 1901: 36, 290, 295 [not *Pecten filosus* Reeve, 1852].
Pecten (Vola) filosus.- Melvill & Standen, 1907: 810 [not *Pecten filosus* Reeve, 1852].
Pecten (Euvola) erythraeensis.- Lamy, 1928: 219; 1938: 13; Barash & Danin, 1972: 361.
Chlamys erythraeensis.- Pallary, 1932: 317.
Pecten benedictus erythraeensis.- Fleming, 1957: 9, 13, 16-18, 33.
Pecten (Oppenheimopecten) erythraeensis.- Grau, 1959: 149; Rombouts, 1991: 54, pl. 20, fig. 3.

Type material: Pecten erythraeensis G.B. Sowerby 2nd: No specimens in the BMNH at London resemble Sowerby's figure or description closely enough to warrant consideration as type material (J. Pickering and K. Way, pers. comm.). The specimen (BMNH 1840.5.18.70) indicated byFleming (1957: pl. 1, fig. 2) as holotype , is neither a type specimen or *P. erythraeensis*.

Type locality: Red Sea, in coral sand.

Material examined: The type material. RED SEA: Ras Matarma, 6 v, HUJ 35598; off Elat, 40-49m, 1 v (fragment), 5.ix.1966, MO 28579; off Elat, 37-49m, 1 v (fragment), 6.ix.1966, MO 28535; Ras Sudr, beach, 3 v, viii.1971, MO 28578; off Ras Abu Rudeis, 29°04'N, 33°02'E, 42-46m, 1 spm., 11.xi.1972, NS 16 466; off Hurghada, 15-20m, live, on sand with eelgrass, 6 spms., HD 3693.

Distribution: Red Sea. Littoral depths, living on soft substrates (mud, sand, coral rubble).

Remarks: Forsskąl (1775: 32) mentioned *Ostrea ziczac* from the Red Sea, and possibly referred to the Linnaean species, known only from the tropical western Atlantic. Chemnitz (1784: 281, fig. 592) also referred to a specimen of *O. ziczac* from the Red Sea, which was in the Spengler collection [ZMUC]. He also mentioned another species from the Red Sea, which was collected by Forsskąl himself (p. 272, pl. 60, figs. 586-7, as a variation of *Pecten maximus* Linnaeus), which is similar to *P. erythraeensis*. This would imply that there are two different *Pecten* species in the Red Sea. However, figure 592 confirms Chemnitz's figures 590-591, which refer to a species from Barbados (West Indies). Subsequently several authors (Dillwyn, 1817, G.B. Sowerby 2nd, 1842, Reeve, 1853, Issel, 1869 and Küster & Kobelt, 1888) cited Forsskąl and Chemnitz, and also recorded the same erroneous locality of the Red Sea.

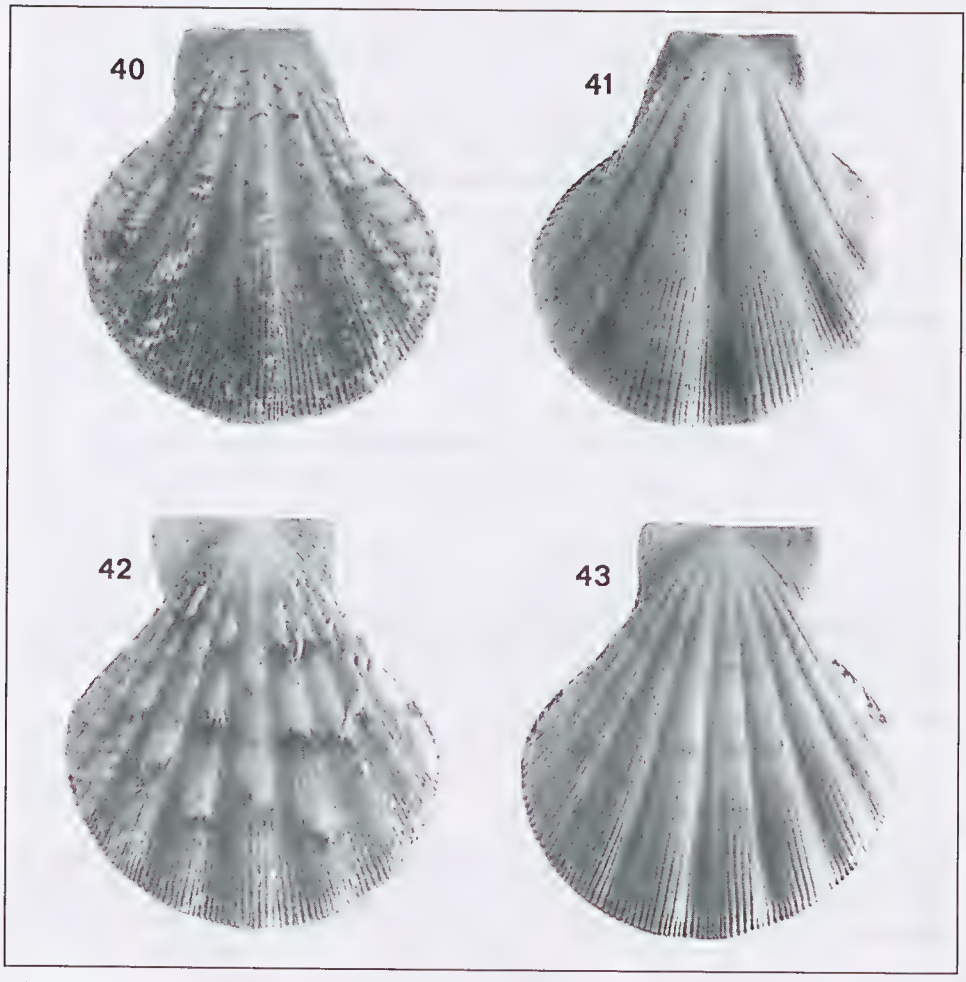


Plate 9.
Figures 40-41. *Decatopecten plica* (Linnaeus, 1758). HD 3327, off Hurghada, 20-40m, H 31.9mm, spm. **40.** lv, exterior. **41.** rv, exterior. **42-43.** *Decatopecten amiculum* (Philippi, 1851). HD 2103, Dahlak Archipelago, 9-12m, H 32.6mm, spm. **42.** lv, exterior. **43.** rv, exterior.

Vaillant (1865), Issel (1869) and Küster & Kobelt (1888), erroneously recorded *Pecten medius* Lamarck from the Red Sea. For further information see Cox (1929: 203).

Melvill & Standen (1907: 810) erroneously recorded from the Gulf of Oman *P. filosus* Reeve, which could be based on *P. erythraeensis* and also described a new species *Pecten dorotheae* from the Persian Gulf. This implies that *P. erythraeensis* has a wider distribution into the coastal waters of the Arabian Sea. However, material from that region has not yet been seen by these authors.

Bosch & Bosch (1982: 159) confused *P. erythraeensis* with typical *P. dorotheae* from Oman, which has angular costae on the right valve instead of rounded ribs, and interstitial commarginal lamellae, which are absent or almost absent in *P. erythraeensis*.

Barnard (1964: 422) recorded a closely allied South African species as *Pecten* cf. *erythraeensis*. Recently Kilburn & Dijkstra (1995) described this species as *Pecten afribenedictus*.

For description of the present species see Oliver (1992: 78).

Subfamily **CHLAMYDINAE** von Teppner, 1922
Tribe **CHLAMYDINI** von Teppner, 1922
Genus **Coralichlamys** Iredale, 1939

Coralichlamys Iredale, 1939: 355.
Type species (by original designation): *Coralichlamys acroporicola* Iredale, 1939 [junior synonym of *Pecten madreporarum* G.B. Sowerby 2nd, 1842]; Recent, tropical Indo-West Pacific.

Diagnosis: Byssally attached Chlamydini, lodged between branches of coral, regularly stenomorphic due to their habitat, with irregular squamose radial primary sculpture, commarginal lamellar secondary sculpture, sometimes with antimarginal striated microsculpture, shagreen microsculpture absent.

Distribution: Miocene - Recent (Hayami, 1989: 15). Tropical Indo-West Pacific. Littoral depths.

Remarks: Hertlein (1969: N355) and Vaught (1989: 118) placed *Coralichlamys* in the synonymy of *Chlamys* Röding, 1798. Waller (1993: 203) treated *Coralichlamys* as an extant genus of Chlamydini.

Coralichlamys madreporarum ([Petit] G.B. Sowerby 2nd, 1842)
(Plate 10, figs. 44-45)

**Pecten madreporarum* [Petit] G.B. Sowerby 2nd, 1842: 68, pl. 14, fig. 68.
**Coralichlamys acroporicola* Iredale, 1939: 356, pl. 5, figs. 26, 26a.
Pecten madreporarum.- Philippi, 1845: 203, pl. 2, figs. 4-5; Reeve, 1853: spec. 117, pl. 28, fig. 117; Küster & Kobelt, 1888: 131, pl. 36, fig. 6.
Pecten (Chlamys) madreporarum.- Adam & Leloup, 1939: 58, pl. 4, fig. 2.
Coralichlamys acroporicola.- Woolacott, 1955: 79, pl. 2, figs. 1-3.

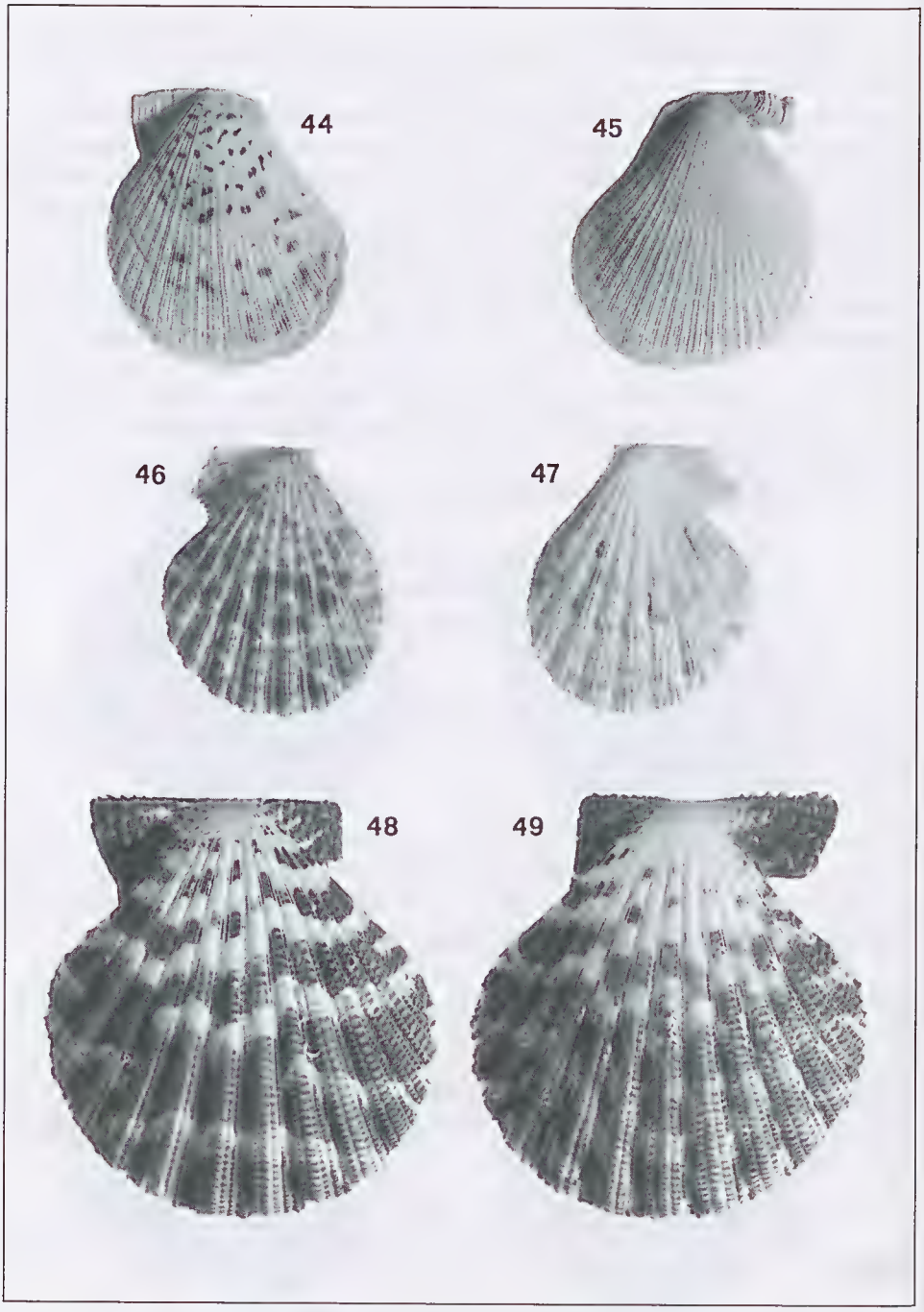


Plate 10.

Figures 44-45. *Coralichlamys madreporarum* (G.B. Sowerby 2nd, 1842). HD 3689, Djibouti, in situ *Acropora* , 18m, H 20.5mm, spm. **44.** lv, exterior. **45.** rv, exterior. **46-47.** *Glorichlamys quadrilirata* (Lischke, 1870). HD 2839, Elat, 20-25m, H 19.8mm, spm. **46.** lv, exterior. **47.** rv, exterior. **48-49.** *Gloripallium pallium* (Linnaeus, 1758). HD 178, off Assab, 2-4m, H 45.8mm, spm. **48.** lv, exterior. **49.** rv, exterior.

Chlamys madreporarum.- Waller, 1972: 238, pl. 3, fig. 42.
Chlamys (Coralichlamys) madreporarum.- Wang, 1983b: 47, pl. 1, fig. 11; Dijkstra, 1986b: 7, illustr. [references]; Rombouts, 1991: 23, pl. 24, fig. 10.
Coralichlamys madreporarum.- Dijkstra, Richer de Forges, Clavier & Lefort, 1990: 7, 8, illustr.

Type material: Pecten madreporarum G.B. Sowerby 2nd: Lectotype BMNH 1995083/1 herein designated, figured by Sowerby (1842: sp. 70, pl. 14, fig. 68), paralectotype BMNH 1995083/2, figured in Reeve (1853: sp. 117, pl. 28, fig. 117) paralectotype BMNH 1995083/3 (not figured); *Coralichlamys acroporicola* Iredale: Holotype AMS C90374.

Type localities: P. madreporarum: "Red Sea" (original description), "Java" (label); *Coralichlamys acroporicola:* Queensland, Low Isles, near Port Douglas.

Material examined: The type material. RED SEA: Elat, 4-8m, in *Acropora* branches, 1 spm., HD 2640. GULF OF ADEN: Djibouti, 18m, in *Acropora* branches, live, 2 spms., HD 1875.

Distribution: Red Sea, Gulf of Aden, Malagasy, Mauritius, Bay of Bengal, eastwards to the Philippines and New Caledonia. Subtidal to shallow sublittoral depths, a coral-dwelling species, lodged amongst *Acropora* branches.

Description: Shell small, up to ca. 30mm height, often stenomorphic or irregular, elongate, oblique, inequivalve, with right valve slightly more convex than left, inequilateral, with auricles unequal, umbonal angle ca. 80-90°.

Both valves sculptured with numerous, irregularly spaced, scabrous fasciated radial riblets. Near ventral margin ribs also have commarginal lamellar microsculpture, near posterior margin sometimes also having interstitial antimarginal microscopic striae. Auricles strongly inequal, anterior much larger in size, with fine radial riblets and commarginal lamellae, posterior with weaker sculpture and strongly dorsally declined.

Byssal notch deep, byssal fasciole rather broad, active ctenolium with 4-6 teeth on suture. Auricular crura broad, resilium strongly triangularly elongate and oblong.

Colour cream or whitish, left valve usually with fine brown maculations, right valve paler and usually without brown interrupted markings.

Remarks: This unique coral-dwelling pectinid could be easily confused with small white specimens of *Laevichlamys rubromaculata* from the northwestern Indian Ocean. However, its habitat (attached between coral branches) sculpture (much more irregular radial riblets) and microsculpture (commarginal lamellae) are different from the latter.

Genus **Laevichlamys** Waller, 1993

Laevichlamys Waller, 1993: 204.

Type species (by original designation): *Pecten multisquamatus* Dunker, 1864; Recent, tropical western Atlantic. For Diagnosis, Distribution and Remarks see Waller (1993: 204).

Laevichlamys rubromaculata (G.B. Sowerby 2nd, 1842)
(Plate 4, figs. 17-19)

-*Pecten rubromaculatus* G.B. Sowerby 2nd, 1842: 67, pl. 13, fig. 34.
Pecten denticulatus A. Adams & Reeve.- Sturany, 1901: 290, 295 [not *P. denticulatus* A. Adams & Reeve, 1850].
Pecten hastatus G.B. Sowerby 2nd.- Vaillant, 1865: 112; Issel, 1869: 102 [not *P. hastatus* G.B. Sowerby 2nd, 1842].
Pecten lividus Lamarck.- Martens, 1880: 314, pl. 22, figs. 6-10 [not *Pecten lividus* Lamarck, 1819].
Pecten serratus G.B. Sowerby 2nd.- Macandrew, 1870: 449; Cooke, 1886: 134 [not *Pecten serratus* G.B. Sowerby 2nd, 1842].
Chlamys rubromaculata.- Viader, 1937: 62.
Chlamys cf. *irregularis* (G.B. Sowerby 2nd).- Mastaller, 1978: 138 [not *Pecten irregularis* G.B. Sowerby 2nd, 1842].
Chlamys lemniscata (Reeve).- Sharabati, 1984: pl. 44, figs. 2, 2a-e [not *Pecten lemniscatus* Reeve, 1853].
Chlamys (Scaeochlamys) lemniscata.- Oliver, 1992: 71, text-figs. 14a-b, 76, pl. 13, figs. 2a-c [not *Pecten lemniscatus* Reeve, 1853].

Type material: Pecten rubromaculatus G.B. Sowerby 2nd: Holotype in F.J. Stainforth collection, which was sold by auction ca. 1850 (Dance, 1986: 166). Type specimen now considered untraceable.

Type locality: Unknown.

Material examined: RED SEA: Elat, 2 spms., 23.ix.1952, NS 2449; Elat, 1 spm., 23.ix.1952, NS 16 474; Ras Gara, 1 spm., 16.x.1972, NS 16 468; Elat, 1 spm., NS 751; Elat, 1 v, NS 752; Elat, 1 spm., HUJ 20694; Elat, 2 v, HUJ 21582; Elat, 2 v, HUJ 21601; Elat, 1 juvenile v, HUJ 21602; Elat, 3 v, HUJ 21605; Elat, 1 spm., HUJ 35742; Aqaba, several v, HUJ 35741; Elat, 2-4m, amongst coral, live, 1 spm., HD 187; Elat, 3-4m, attached to coral, sand, live, 1 spm., HD 428; Elat, 8-12m, under rocks and corals, sand, live, 3 spms., HD 778; Elat, 6-10m, amongst corals, sand, live, 3 spms., HD 1515; Elat, 6-10m, amongst coral rubble, live and dead, 3 spms., HD 2902; Elat, 6-7m, attached amongst coral, live, 1 juvenile spm., HD 2907; Elat, 4-9m, amongst corals, live, 4 spms., HD 2909; 30km S of Elat, 6-8m, attached to corals, live, 5 spms., HD 1352; S of Elat, 4-10m, amongst corals, 2 spms., HD 2906; Elat, 4 spms., 3 v, 1964/65, ZMUC. GULF OF ADEN: Djibouti, 24-28m, under coral slabs and amongst coral rubble, soft sediments, live and dead, several specimens, HD 2900; Aden, Arosat al Baher, beach, 1 spm., HD 2903. SEYCHELLES: 18-26m, amongst coral rubble, soft sediments, live and dead, 7 spms., HD 2918.

Distribution: Red Sea, Gulf of Aden, Seychelles, Chagos Islands, southwards to

Réunion and Mauritius. Littoral depths, living byssally attached to coral branches or underside of boulders or amongst coral rubble on sandy bottoms.

Remarks: The present species differs from the closely related species *Laevichlamys lemniscata* (Reeve, 1853), known from the southwestern Indian Ocean to South Africa, by a finer sculpture of radial costae and lamellae, in colouration and in size [*L. rubromaculata* up to ca. 40mm; L. lemniscata ca. 60mm].

For description of the present species see Oliver (1992: 76) [as *Chlamys (Scaeochlamys) lemniscata* (Reeve, 1853)].

Laevichlamys superficialis (Forsskål, 1775)
(Plate 5, figs. 20-21)

**Ostrea superficialis* Forsskål, 1775: 123, no. 60.
Pecten sulphureus Chemnitz, 1784: 328, pl. 66, fig. 629 [not binomial].
Ostrea sanguinea Dillwyn [not Linnaeus, 1758], 1817: 259 [in part].
---------- Savigny, 1817: pl. 13, fig. 7.
Pecten --------- Audouin, 1828: 208, pl. 13, fig. 7.
Pecten lividus Lamarck [in part].- G.B. Sowerby 2nd, 1842: 69, pl. 13, fig. 61, pl. 14, figs. 89, 91; Issel, 1869: 103; Macandrew, 1870: 449; Pagenstecher, 1877: 29; Paetel, 1890: 231; Smith, 1891: 434 [in part]; Sturany, 1901: 290, 295; Mastaller, 1978: 138.
Pallium superficialis.- Mörch, 1853: 58 [in part].
Pecten laetus Gould.- P. Fischer, 1870: 168 [not Gould, 1850].
Pecten squamosus (Gmelin) [in part].- Martens, 1880: 314; Shopland, 1902: 171; Anthony, 1905: 499; Tillier & Bavay, 1905: 177; Steinitz, 1929: 72; Ryland, 1951: 16; Mastaller, 1978: 138.
Pecten squamosus var. *lividus*.- Shopland, 1896: 235.
Pecten (Chlamys) squamosus [in part].- Dautzenberg & Bavay, 1912: 14.
Chlamys livida.- Pallary, 1926: 121, pl. 13, figs. 7.1-7.4; Sharabati, 1984: pl. 44, figs. 5, 5a.
Chlamys squamosa var. *sulphurea* (Gmelin).- Lamy, 1928: 169.
Chlamys squamosa var. *decoriata* [Jousseaume] Lamy, 1928: 170; Moazza, 1939: 33.
Chlamys squamosa.- Cox, 1929: 206; Franc, 1956: 54; Barash & Danin, 1972: 361; Sharabati, 1984: pl. 44, figs. 3, 3a-d; Taylor & Reid, 1984: 206.
Chlamys decoriata.- Pallary, 1932: 317.
Chlamys ruschenbergeri Tryon.- Lamy, 1935: 308; Bosch & Bosch, 1982: 160, illustr. [not *Pecten ruschenbergerii* Tryon, 1869].
Ostrea superficialis.- Yaron, Schiøtte & Wium-Andersen, 1986: 181, fig. 23.
Chlamys (Scaeochlamys) superficialis.- Oliver, 1992: 71, 75, pl. 13, figs. 3a-c, text-fig. 11.

Type material: 4 syntypes (articulated specimens) ZMUC BIV-321; one syntype (articulated specimen) ZMUC BIV-322 depicted by Yaron, Schiøtte & Wium-Anderson (1986: 181), possible syntypes (13 valves) ZMUC BIV-320.

Type locality: Egypt, Suez.

Material examined: The type material. EGYPT: Small Bitter Lake [Buheirat-Murrat-el-Sughra], 1 v, HUJ 21583. RED SEA: Suez, 1 v, HUJ 35750; Suez, 1-2m, attached under rock, live, 2 juvenile spms., HD 3105; El Bilaiyim, 1 spm., HUJ 35601; Elat, intertidal, 1 spm., 26.v.1971, MO 28583; Bilaiyim Lagoon, 1 v, 24.viii.1971, MO 28533; Bilaiyim Lagoon, 1 spm., 24.viii.1971, MO 28580; Bilaiyim Lagoon, 3 spms., 28.ix.1971, NS 16 455; Bilaiyim Lagoon, 1 spm., 27.x.1971, NS 8479; Elat, 5 v, HUJ 21603; Elat, 1 spm., HUJ 35747; Elat, 1 spm., HUJ 35748; Elat, 2-4m, under stone, live, 1 spm., HD 170; Elat, 2-4m, attached to rock, live, 1 spm., HD 405; off Elat, 1-3m, attached under rocks, live, 5 spms., HD 1599; off Elat, 4-6m, under coral, live, 2 spms., HD 1600; off Elat, 0.5-2m, attached under rocks and corals, live, several spms., HD 3301; off Elat, 1-3m, under coral boulder, live, 4 spms., HD 3302; Elat, 1 spm., 1954/65, ZMUC; Aqaba, 2 v, HUJ 35749; S of Elat, 6-8m, amongst coral rubble, live, 1 spm., HD 388; Dahab, 15m, among rubble, 1 spm., HD 3716; Ras Burqa, 8-10m, 1 juvenile v, HUJ 35653; Et Tor, 1 spm., HUJ 35751; Umm Aabak, 3 spms., HUJ 21604; Dahlak Archipelago, 1 spm., HUJ 21606.

Distribution: Red Sea. Subtidal to littoral depths, living byssally attached to rocks, stones or coral boulders on sandy bottoms.

Remarks: O. superficialis Forsskål was overlooked by many authors. Only Mörch (1853) mentioned *Pallium superficialis* Forsskål from the Red Sea. *Laevichlamys ruschenbergeri* (Tryon, 1869) from the northwestern Indian Ocean is closely related to *L. superficialis*; the former species attaining larger size (up to ca. 100mm), and being slightly more convex with a finer sculpture, and a more prominent shagreen microsculpture.

For description of the present species see Oliver (1992: 75).

Subfamily **PEDUMINAE** Habe, 1977
Tribe **HINNITINI** Vaught, 1989 [no diagnosis]
Genus **Pedum** Lamarck, 1799

Pedum Lamarck, 1799: 88.
Type species (by monotypy; subsequent designation by Schmidt, 1818): *Ostrea spondyloidea* Gmelin, 1791; Recent, Indo-West Pacific.

Diagnosis: Dorso-ventrally elongated Hinnitini, attached in crevices of living corals, left valve rather flat, right valve convex, microscopically sculptured with scabrous radial riblets and closely arranged commarginal lamellae, anterior auricle in mature stage strongly curved, posterior nearly absent, resilial insertions high, narrow and oblong, byssal fasciole broad, byssal gape very wide, ctenolium present only in juvenile examples, absent in mature shells.

Distribution: Recent (Waller, 1972: 258; Hayami, 1989: 16); tropical Indo-Pacific; littoral and shallow sublittoral depths.

Remarks: Hertlein (1969: N364) placed *Pedum* in the suprageneric *Hinnites* group, Vaught (1989: 119) in Hinnitini. Habe (1977: 92) established a new subfamily Peduminae of Pectinidae.

Pedum spondyloideum (Gmelin, 1791)
(Plate 5, figs. 23-24)

**Ostrea spondyloidea* Gmelin, 1791: 3335, no. 109.
**Pedum pedum intensum* Iredale, 1939: 340.
---------- Favanne, 1780: pl. 80, fig. K.
Ostrea spondyloidea Chemnitz, 1785: 28, pl. 72, figs. 669-670 [invalid publication]; Dillwyn, 1817: 280.
Pedum spondyloides.- Lamarck, 1799: 88.
Pedum spondyloideum.- Lamarck, 1817: 154; Quoy & Gaimard, 1835: 447, pl. 76, figs. 15-21; Reeve, 1841: 154, pl. 111, figs. 1-5; 1860: 61, pl. 28, fig. 164, pl. N, fig. 3; G.B. Sowerby 2nd, 1842: 438, pl. 91, figs. 1-4; Chenu, 1843: 1, pl. 1, figs. 1-3; Sganzin, 1843: 11; Mörch, 1853: 61; P. Fischer, 1858: 340; Chenu, 1862: 189, fig. 961; Issel, 1869: 105; Macandrew, 1870: 450; Martens, 1880: 313; Cooke, 1886: 136; Shopland, 1896: 235; 1902: 179; Sturany, 1905: 141; Lamy, 1928: 220; Cox, 1929: 207; Kuroda, 1931: 82; Lamy, 1935: 306; Viader, 1937: 62; Yonge, 1967: 311, figs. 1-8; Hertlein, 1969: 364; Habe, 1964: 174, pl. 53, fig. 15; 1977: 92; Waller, 1972: 226, 230, 254, pl. 8, figs. 136-143, figs. 21B, 22; Mastaller, 1978: 138; 1979: 142; Mergner, 1979: 481, 500; Oliver, 1982: 14; Taylor & Reid, 1984: 183, 206; Dijkstra, 1987b: 9, illustr.; 1991b: 40; 1997: 332, fig. 41; Nielsen, 1986: 8, figs. 3A-B [holotype]; Oliver, 1992: 69, 78, text-fig. 1, pl. 14, fig 5a-c; Bernard, Cai & Morton, 1993: 53.
Pedum sp. Mastaller, 1978: 127, 138.

Type material: Ostrea spondyloidea: Holotype ZMUC BIV-57; *Pedum pedum intensum:* Holotype AMS C90353.

Type localities: Ostrea spondyloidea: India; *Pedum pedum intensum:* N Queensland, Low Isles, anchorage, in *Porites*.

Material examined: RED SEA: Elat, 1 juvenile spm., HUJ 30482; Elat, 1 spm., HUJ 30483; Elat, 6 juvenile spms., HUJ 30484; Aqaba, 2 v, HUJ 35740. GULF OF ADEN: Djibouti, 10-18m, in coral, dead, 7 spms., HD 3702; Djibouti, 24-26m, in coral, live and dead, 3 spms., HD 3703.

Distribution: Red Sea, Gulf of Aden, eastcoast of Africa to Natal (South Africa), Malagasy, Réunion, Mauritius, eastwards to southern Japan and French Polynesia. Living in fissures generally of massive coral heads of *Porites* in shallow water.

Remarks: Examined specimens of *P. spondyloideum* from the Red Sea are morphologically similar to the holotype. *P. spondyloideum* is extremely variable in shape, due to stenomorphic development in fissures of living corals.

For description and further information on morphology, ecology and distribution see Yonge (1967), Waller (1972), Nielsen (1986) and Kleemann (1990).

Genus **Semipallium** [Jousseaume] Lamy, 1928

Semipallium [Jousseaume] Lamy, 1928: 169.
Type species (by monotypy): *Pecten tigris* Lamarck, 1819; Recent, W Indian Ocean, Indo-West Pacific. For diagnosis, distribution and remarks see Dijkstra & Kastoro (1997: 268).

Semipallium crouchi (E.A. Smith, 1892)
(Plate 6, fig. 29)

**Pecten crouchi* Smith, 1892: 255, fig.
Pecten luculentus Reeve, var.- Smith, 1891: 434; Shopland, 1896: 234; Sturany, 1901: 295. [not Reeve, 1853]
Chlamys fulvicostata (A. Adams & Reeve).- Cox, 1929: 204 [not A. Adams *in* A. Adams & Reeve, 1850].
Manupecten tigris var. *crouchi*.- Lamy, 1935: 312.
Chlamys crouchi.- Viader, 1937: 61.
Complicachlamys crouchi.- Iredale, 1939: 363.
Chlamys luculenta (Reeve, 1853).- Rees & Stuckey, 1952: 198; Mastaller, 1979: 140 [not Reeve, 1853].
Semipallium crouchi.- Dijkstra, 1984a: 3-4; Rombouts, 1991: 58, pl. 20, fig. 12; Oliver, 1992: 72 (text-figs. 19a-b), 77, pl. 12, figs. 10a-b.
Semipallium fulvicostatum.- Sharabati, 1984: pl. 44, fig. 7 [not Adams & Reeve, 1850].

Type material: Lectotype BMNH 1892.9.25.1 herein designated, possible paralectotype BMNH 1892.1.11.16.

Type locality: Mauritius.

Material examined: RED SEA: Elat, opposite Old Port, 121m, 2 v, 10.IX.1968, MO 28478; Elat, 20m, 2 spms., HUJ 20693; Gulf of Aqaba, 30-35m, 1 v, HUJ 35596; Elat, harbour, 1 v, HUJ 35607; off Elat, 12m, sand and rubble, 1 spm., HD 1597; off Elat, 21m, sand and coral rubble, 1 spm., HD 2040; off Elat, 25-30m, attached to rock, live, 1 spm., HD 2042; Aqaba, 10-12m, among coral rubble, live, 1 spm., HD 180; S of Aqaba, 15m, amongst coral, live, 1 spm., HD 399; 175km S of Elat, 22m, on coral, 1 spm., HD 913; 200km S of Elat, 20 m, amongst coral rubble, sand, live, 1 spm., HD 2041.

Distribution: Red Sea, northern east coast of South Africa, Réunion, and Mauritius. Littoral to sublittoral depths, living byssally attached to dead or living corals or amongst coral rubble on sandy substrates.

Remarks: Philippi (1845: 101) recorded *Pecten tigris* Lamarck, 1819 from the Red Sea, and referred to Chemnitz (1784, fig. 608). Chemnitz's figure, however represents *Gloripallium maculosum* (Forsskål). Issel (1869: 103) also mentioned *P. tigris* from the Red Sea, and referred to Philippi's description and figure. At

present no records of *Semipallium tigris* are known from the Red Sea, although specimens have been examined from Mauritius, Réunion (MNHN) and South Africa (NM).

Smith (1891: 434) and Shopland (1896: 234) cited a variety of *Pecten luculentus* Reeve from Aden. This form could be *S. crouchi.*

Sturany (1901: 295) and Rees & Stuckey (1952: 198) also recorded *P. luculentus* from the Gulf of Aqaba and the Red Sea. This should be *P. crouchi.* They neglected or overlooked Smith's description.

Cox (1929: 204) reported *Chlamys fulvicostata* (Adams & Reeve) from the Red Sea and synonymized with it *Pecten luculentus* Reeve, 1853. He followed the opinion of Dautzenberg & Bavay (1912: 16-17), who also placed *Pecten dringi* Reeve, 1853, in that synonymy. We consider that *Semipallium dringi,* from the Indo-West Pacific, however, is a valid species (see Dijkstra, 1991b: 39).

The conchological characters of *Semipallium dianae* (Crandall, 1979) from the Indo-West Pacific, are closest to the present species (Dijkstra, 1991b: 38).

For description of the present species see Oliver (1992: 77).

Tribe **MIMACHLAMYDINI** Waller, 1993
Genus **Mimachlamys** Iredale, 1929

Mimachlamys Iredale, 1929: 162.
Type species (by original designation): *Pecten asperrimus* Lamarck, 1819; Recent, southern Australia.

Diagnosis: Non-cemented, byssally attached Mimachlamydini, shell convex with regularly placed, primary squamous radial ribs, flanked by secondary radial riblets; granulated microsculpture in early ontogeny, interstitial microsculpture divaricate or antimarginal near antero- and postero-ventral margins; auricles unequal, byssal notch relatively deep, byssal fasciole rather broad, ctenolium well developed.

Distribution: Eocene - Recent (Waller, 1991: 32); Indo-West Pacific and eastern Atlantic (Waller, 1991: 31); intertidal to shallow sublittoral depths.

Remarks: Hertlein (1969: N355) placed *Mimachlamys* in the synonymy of *Chlamys* Röding, 1798, as did Vaught (1989: 118). Waller (1991: 31; 1993: 200) established the morphological differences between *Chlamys* and *Mimachlamys,* and placed the latter genus in the tribe Mimachlamydini.

Mimachlamys andamanica (Preston, 1908)
(Plate 4, figs. 14-15)

**Chlamys andamanica* Preston, 1908: 204, pl. 14, fig. 19.
**Pecten perfectus* Melvill, 1909: 127, pl. 5, fig. 15.
Chlamys perfecta.- Viader, 1937: 62; Oliver, 1982: 7; Dijkstra, 1986a: 9, illustr.
Pecten perfectus.- Trew, 1987: 56.
Chlamys andamanica.- Dijkstra, 1991b: 29, fig. 90.

Type material: Chlamys andamanica Preston: Holotype ZSI M4042/1; *Pecten perfectus* Melvill: Holotype BMNH 1910.3.17.22.

Type localities: Chlamys andamanica: Bay of Bengal, Andaman Islands; *Pecten perfectus:* Indian Ocean, Chagos Archipelago, Peros Banhos, Diamant, 16 fathoms [29m].

Material examined: RED SEA: off Elat, 60-90m, 2 v, 5.ix.1966, MO 28442; off Elat, 62-80m, 1 v, 7.ix.1966, MO 28439; Elat, off Old Port, 121m, 3 v, 10.ix.1968, MO 28441; Elat, off Old Port, 121m, 1 v, 10.ix.1968, MO 28437; Elat, off Zarhin Plant., 167m, 1 v, 16.ix.1968, MO 28438; off Mersat Abu Samra, 46-49m, 5 v, 6.x.1969, MO 28440; off Mersat Abu Samra, 46-49m, 1 v, 6.x.1969, MO 28435; off Nuweiba el Tarabin, 137-146m, 1 v, 8.x.1969, MO 28443; Elat, opposite New Port, 170-270m, 1 v, 13.ii.1970, MO 28466; Elat, opposite Old Port, 300-420m, 1 v, 13.ii.1970, MO 28436; Elat, harbour, 1 v, HUJ 35590; Elat, 9-11m, under rocks, sand, live, 3 spms., HD 2141; Elat, 1.5m, in coral rubble, live, 3 spms., HD 2142; Elat, 9-10m, on sand, 1 spm., HD 2143; Elat, 15-20m, among coral rubble, live, 2 spms., HD 2145; Elat, 7-8m, among coral rubble, live, 1 spm., HD 2146. GULF OF ADEN: Yemen, off Hadibo, 18m, among rubble, live, 2 spms., HD 2151.

Distribution: Red Sea, Seychelles, Chagos Islands, Mauritius, Andaman Islands, Indonesia and New Caledonia. Tropical shallow waters, living byssally attached under rocks and coral boulders, or amongst coral rubble on sandy substrates.

Description: Shell convex, thin, up to ca. 30mm high, elongate, unusually oblong, almost equivalve and equilateral; auricles unequal, sculptured with many closely spaced squamous radial riblets, ca. 25 in immature stage and increasing to ca. 60 in the adults near the ventral margin on both valves; interstitial microsculpture somewhat granulated in early ontogeny, developed into divaricate scratches in late ontogeny near antero- and postero-margins; anterior auricles sculptured with prominent squamose radial riblets crossed by commarginal lamellae, byssal notch rather deep, byssal fasciole broad, ctenolium well developed with ca. 6-8 active teeth.

Colour variable, red, orange, yellow, purple or brown, with light and dark maculations and striations, sometimes uniform in colour.

Remarks: This species is a new record for the Red Sea fauna. The Red Sea shells are slightly different from the type material of *Mimachlamys andamanica*. The interstices of the regular antimarginal costae of the left valve are somewhat broader and the microscopic divaricate striae between the radial costae are more prominent. The anterior auricle has a few more riblets with a finer sculpture. The sculpture of the right valve is similar to the type material. Red Sea shells are usually uniformly red or occasionally orange in contrast to typical specimens, which are much more variable in colour.

Melvill (1909) described *Pecten perfectus* from the Chagos Archipelago of the central Indian Ocean, which is clearly conspecific with the type material of *Mimachlamys andamanica*.

Mimachlamys deliciosa Iredale, 1939 from the western Pacific (Japan to Australia) is closely related and lives in deeper waters. It is more oval in shape, and sculptured with more irregularly arranged radial riblets.

Mimachlamys senatoria (Gmelin, 1791)
(Plate 4, fig. 16)

**Ostrea senatoria* Gmelin, 1791: 3327.
**Ostrea porphyrea* Gmelin, 1791: 3328.
**Pecten aurantius* Lamarck, 1819: 175.
**Pecten florens* Lamarck, 1819: 175.
**Pecten indicus* Deshayes, 1832: 410, pl. 3, fig. 5.
**Pecten pseudolima* G.B. Sowerby 2nd, 1842: 78, pl. 20, fig. 235.
**Pecten layardi* Reeve, 1853: sp. no. 80, pl. 21, figs. 80a-b.
**Pecten fricatus* Reeve, 1853: sp. no. 161, pl. 34, fig. 161.
**Pecten blandus* Reeve, 1853: sp. no. 162, pl. 34, figs. 162a-b.
**Pecten raffrayi* Jousseaume, 1886: 221, fig.
**Mimachlamys ellochena* Iredale, 1939: 349, pl. 5, fig. 24.
**Chlamys (Mimachlamys) asperrimoides* Powell, 1958: 70, pl. 11, figs. 3-4, text fig. 3.
Pallium senatoris Chemnitz, 1784: 320, pl. 65, fig. 617 [not binomial].
Pallium porphyreum Chemnitz, 1784: 330, pl. 66, fig. 632 [not binomial].
Ostrea senatoria.- Dillwyn, 1817: 256.
---------- Savigny, 1817: pl. 13 fig. 5.
Pecten senatorius.- Lamarck, 1819: 174; Deshayes, 1836: 146; G.B. Sowerby 2nd, 1842: 74, pl. 17, fig. 151, pl. 18, figs. 188-192; Reeve, 1853: spec. 81, pl. 21, fig. 81; Issel, 1869: 102; Macandrew, 1870: 449; P. Fischer, 1871: 209; Lienard, 1877: 69; Cooke, 1886: 134; Jousseaume, 1888: 220; Küster & Kobelt, 1888: 63, pl. 16, fig. 7; Smith, 1891: 434; Shopland, 1896: 235; 1902: 171; Smith, 1903: 621; Sturany, 1905: 141; Anthony, 1906: 498; Melvill & Standen, 1907: 809; Lynge, 1909: 57.
Pecten ---------- Audouin, 1826: 54, pl. 13, fig. 5.
Pecten aurantius.- Deshayes, 1836: 146.
Pecten florens.- Deshayes, 1836: 147; Küster & Kobelt, 1888: 82, pl. 16, fig. 8, pl. 20, fig. 3.
Pecten pseudolima.- Reeve, 1853: sp. no. 57, pl. 16, figs. 57a-b.
Pecten porphyreus.- Philippi, 1845: 101; Martens, 1880: 314; Tillier & Bavay, 1905: 178; Melvill, 1909: 127; Pallary, 1926: 121, pl. 13, fig. 5.
Pecten australis G.B. Sowerby 2nd.- Vaillant, 1865: 112; Issel, 1869: 102, 259, 372; Pagenstecher, 1877: 29; Jousseaume, 1888: 220; Sturany, 1901: 290, 295 [not G.B. Sowerby, 1842].
Pecten miniaceus Lamarck.- Issel, 1869: 383 [not Lamarck, 1819].
Pecten senatorius (Gmelin) var.- Smith, 1885: 300.
Pecten splendidulus G.B. Sowerby 2nd.- Jousseaume, 1888: 221.
Pecten layardi Reeve var.- Shopland, 1896: 234.
Pecten layardi.- Shopland, 1902: 171; Melvill & Standen, 1907: 808.
Pecten (Chlamys) senatorius.- Dautzenberg & Bavay, 1912: 4 [synonymy].
Chlamys porphyrea.- Pallary, 1926: 121, pl. 17, figs. 5.1-4.
Chlamys porphyreus.- Tomlin, 1927: 300; Pallary, 1932: 317.

Chlamys senatoria.- Lamy, 1928: 166; 1935: 307; 1938: 12; Cox, 1929: 206; Viader, 1937: 62; Eames & Cox, 1956: 14, 40; Barnard, 1964: 430; Smythe, 1972: 495; Selli, 1973: 181 [references]; Mastaller, 1979: 141; 1987: 210; Abbott & Dance, 1982: 309, illustr.; Bosch & Bosch, 1982: 160; Glayzer, Glayzer & Smythe, 1939: 325; Sharabati, 1984: pl. 44, fig. 8; Oliver, 1992: 72, text-figs. 17a-c, 18a-b, 74, pl. 13, figs. 1a-b [synonymy, description]; Bosch, Dance, Moolenbeek & Oliver, 1995: 230.
Chlamys senatoria var. *porphyrea*.- Lamy, 1928: 166; 1938: 12 [not G.B. Sowerby, 1842].
Chlamys senatoria var. *australis* (G.B. Sowerby 2nd).- Lamy, 1928: 167; 1938: 12.
Chlamys (Aequipecten) porphyreus.- Dautzenberg, 1929: 561; Moazzo, 1939: 34.
Mimachlamys senatoria.- Dijkstra, 1991b: 34 [synonymy]; 1997: 326, figs. 22-23; Waller, 1991: 32, pl. 4, figs. 3, 6; Dijkstra & Marshall, 1997: 101, pl. 9, figs. 1-4.
Chlamys (Mimachlamys) senatoria.- Rombouts, 1991: 30, pl. 11, figs. 6, 6a.
Mimachlamys asperrimoides.- Lamprell & Whitehead, 1992: [text unpag.], pl. 10, fig. 57.

Type material: Ostrea senatoria Gmelin: Lectotype designated by Dijkstra & Marshall (1997: 102) ZMUC BIV-45;
Ostrea porphyrea Gmelin: Lectotype (lv) designated by Dijkstra & Marshall (1997: 102) ZMUC BIV-46, paralectotype (rv) ZMUC BIV-47;
Pecten aurantius Lamarck: Lectotype designated and figured by Dijkstra (1994: 489, figs. 106-110) MNHN [not registered];
Pecten florens Lamarck: Holotype MHNG 1088/70;
Pecten indicus Deshayes: Type material not found;
Pecten pseudolima G.B. Sowerby 2nd: 3 syntypes BMNH 1950.11.14.54-56;
Pecten layardi Reeve: 6 syntypes BMNH 1994.162;
*Pecten fricatus*Reeve: Holotype BMNH 1994.161; *Pecten blandus* Reeve: 5 syntypes BMNH 1950.11.14.13-17;
Pecten raffrayi Jousseaume: Holotype MNHN [not registered];
Mimachlamys ellochena Iredale: Holotype AMS C.119511;
Chlamys (Mimachlamys) asperrimoides Powell: Holotype AIM TM.1235, paratype ZMUC.

Type localities: Ostrea senatoria: 'Oceano Indico' [Indian Ocean];
Ostrea porphyrea: "Mari rubro" [Red Sea];
Pecten aurantius: "l'Océan indien?" [Indian Ocean?];
Pecten florens: "l'Océan indien?" [Indian Ocean?];
Pecten indicus: "Ceylan" [Sri Lanka];
Pecten pseudolima: Jacna, Bohol, Philippines;
Pecten layardi: "Ceylon" [Sri Lanka];
Pecten fricatus: Locality unknown;
Pecten blandus: Australia;
Pecten raffrayi: Zanzibar;
Mimachlamys ellochena: G.B.R. stn. XVII, off Shaw Islands, Whitsunday Group, Queensland, 37m;
Chlamys (Mimachlamys) asperrimoides: "Galathea" stn. 674, 29°15'S, 177°57'W, off

Raoul Island, Kermadec Islands, 75-85m.

Material examined: The type material. EGYPT: Small Bitter Lake [Buheirat-Murrat-el-Sughra], 2 v, HUJ 21583. RED SEA: off Suez, 22-24m, among sand and rubble, live, 2 juvenile spms., HD 2983; Ras Matarma, 1 v, HUJ 35599; off Hurghada, 15-20m, soft substrates, eelgrass, live, 5 spms., HD 3711; Dvulkurush, 59m, 2 v, HUJ 35586; Ethiopia, 1 v, HUJ 35746; Ethiopia, Massawa Channel, 2 spms. + 1 v, HUJ 35585; Dahlak Archipelago, 15°35'N, 40°44'E, 36m, 1 spm., 13.x.1965, ISRSE 2544; Dahlak Archipelago, 15°17'N, 40°10'E, 18-20m, 1 v, 16.x.1965, ISRSE 0155; Dahlak Archipelago, 15°17'N, 40°10'E, 18-20m, 3 spms., 16.x.1965, ISRSE 1758; Dahlak Archipelago, 15°17'N, 40°10'E, 18-20m, 1 v, 16.x.1965, ISRSE 0166; Dahlak Archipelago, 14°58'N, 40°19'E, 9-12m, 1 spm., 17.x.1965, ISRSE 1430; Dahlak Archipelago, 14°58'N, 40°19'E, 9-12m, 1 v, 17.x.1965, ISRSE 1431; Dahlak Archipelago, 14°58'N, 40°19'E, 9-12m, 2 v, 17.x.1965, ISRSE 1454; Dahlak Archipelago, 15°08'N, 40°18'E, 9m, 1 v (juv.), 17.x.1965, ISRSE 1408; Dahlak Archipelago, 14°58'N, 40°19'E, 9-12m, 1 spm., 17.x.1965, ISRSE 1430; Dahlak Archipelago, 15°35'N, 40°40'E, 20-24m, 2 spms., 22.x.1965, ISRSE 1695b; Dahlak Archipelago, 15°37'N, 40°43'E, 55m, 2 spms., 4 v, 23.x.1965, ISRSE 1853; Dahlak Archipelago, 15°37'N, 40°43'E, 55m, 23 spms., 23.x.1965, ISRSE 1883; Dahlak Archipelago, 15°30'N, 40°43'E, 55m, 14 spms., 23.x.1965, ISRSE 1884; Dahlak Archipelago, Hatitou, 22-26m, 10 spms., x.1965, ISRSE 2593; Dahlak Archipelago, 6 v, 1965, MO 28434; Dahlak Archipelago, 40-45m, soft sediments, live, 11 spms., HD 3710; Yemen, Al Khawkhah, live, 2 spms., HD 5996; Massawa, 1 v, HUJ 35745; Ras Sudr, beach, 1 v, 25.x.1971, NS 8571. GULF OF ADEN: Yemen, Ras Umran, beach, 2 v, HD 2980; Yemen, off Hadibo, 23m, soft substrates, live, 2 spms., HD 2982; Yemen, off Fugum, 15m, soft substrates, live, 1 spm., HD 3699; Yemen, Mocca, beach, 3 v, HD 3766. SOMALIA: Bocaso, beach, 2 v, HD 3001; off Ras Hafoun, 40m, sand, live, 1 spm., HD 3722.

Distribution: Red Sea, Gulf of Aden, east coast of Africa to South Africa, Arabian Sea, Persian Gulf, extending eastwards to the Philippines and New Caledonia. Subtidal to sublittoral depths, living byssally attached to rocks or amongst sponges on soft sediments (mud, sand and rubble).

Remarks: M. senatoria is very variable in form, sculpture and colour. Red Sea specimens are often covered with sponges (van Soest, 1994), viz. *Callyspongia* or *Mycale* [det. R.W.M. van Soest, ZMA].

For description of the present species see Oliver (1992: 74).

Tribe **AEQUIPECTININI** von Teppner, 1922
Genus **Cryptopecten** Dall, Bartsch & Rehder, 1938

Cryptopecten Dall, Bartsch & Rehder, 1938: 93.
Type species (by original designation): *Cryptopecten alli* Dall, Bartsch & Rehder, 1938 [junior synonym of *Pecten (Chlamys) bullatus* Dautzenberg & Bavay, 1912] (Hayami, 1984: 88); Recent, Hawaiian Islands.

For synonymy, diagnosis and distribution see Hayami (1984: 88) and Dijkstra (1995: 60).

Cryptopecten nux (Reeve, 1853)
(Plate 3, figs. 12-13)

**Pecten coruscans* Hinds.- Reeve, 1853: spec. 143, pl. 32 fig. 143 [not Hinds, 1845].
Pecten nux Reeve, 1853: errata.
**Pecten hastingsii* Melvill, 1888: 279, pl. 2, fig. 7.
**Pecten guendolenae* Melvill, 1888: 279, pl. 2, fig. 6.
**Chlamys smithi* G.B. Sowerby 3rd, 1908: 18, pl. 1, figs. 6-7.
**Chlamys corymbiatus* Hedley, 1909: 423, pl. 36, figs. 1-4.
-Pecten (Aequipecten) kikaiensis Nomura & Zinbo, 1934: 153, pl. 5, figs. 9a-b.
Pecten nux.- Küster & Kobelt, 1888: 163, pl. 45, figs. 5-8; Paetel, 1890: 232; Smith, 1903: 621; Smith, 1904: 13; Lynge, 1909: 155; Melvill, 1909: 127.
Pecten (Aequipecten) vesiculosus Dunker.- Dautzenberg & Bavay, 1912: 148 [not Dunker, 1877].
Chlamys (Aequipecten) nux.- Cox, 1930: 124, pl. 14, fig. 11; Eames & Cox, 1956: 43.
Chlamys nux.- Dautzenberg & Bouge, 1933: 427; Viader, 1937: 62.
Pecten (Aequipecten) nux.- Nomura, 1933: 55; Nomura & Zinbo, 1934: 117 [in part].
Aequipecten nux.- Lamy, 1935: 315.
Chlamys smithi.- Viader, 1937: 62.
Cryptopecten nux.- Habe, 1951: 77; 1961: 118, pl. 53, fig. 9; 1964: 174, pl. 53, fig. 9; 1977: 84; Kira, 1962: 174, pl. 53, fig. 9; Hayami, 1982: 235; Wang, 1983a: 403, figs. 1 (8-13); Hayami, 1984: 99, pl. 2, fig. 4, pl. 3, figs. 1-2, pl. 9, figs. 2-5, pl. 12, figs. 1-2 [synonymy, references, description, distribution, discussion]; Dijkstra, 1991b: 36; Lamprell & Whitehead, 1992: pl. 11, fig. 66; Bernard, Cai & Morton, 1993: 50 [distribution].
Chlamys (Cryptopecten) nux.- Shikama, 1964: 50, fig. 93.
Cryptopecten kikaiensis.- Habe, 1977: 84.
Cryptopecten hastingsii.- Habe, 1977: 85.
Pecten guendolenae.- Trew, 1987: 43.
Pecten hastingsii.- Trew, 1987: 44.
Cryptopecten bernardi corymbiatus.- Dijkstra, 1988b: 7, illustr.
Cryptopecten bernardi nux.- Dijkstra *et al.*, 1990: 9, 10, illustr.
Chlamys (Cryptopecten) bernardi.- Rombouts, 1991: 23, pl. 23, figs. 3, 3a; Oliver, 1992: 72, text-figs. 21a-b, 76, pl. 14, figs. 3a-b. [not Philippi, 1851].

Type material: Pecten nux Reeve: Lectotype BMNH 1950.11.14.52, 2 paralectotypes BMNH 1950.11.14.50-51 designated by Wagner (1989);
Pecten hastingsii Melvill: Holotype NMW 1955.158.10;
Pecten guendolenae Melvill: Holotype NMW 1955.158.02;
Chlamys smithi G.B. Sowerby 3rd: Holotype BMNH 1908.5.30.63;
Chlamys corymbiatus Hedley: 2 syntypes AMS C.27532;
Pecten (Aequipecten) kikaiensis Nomura & Zinbo: Holotype (rv) IGPS 50357.

Type localities: Pecten nux: Philippines, Bohol, Panglao [restricted by Wagner, 1989];

Pecten hastingsii: Japan;
Pecten guendolenae: Mauritius;
Chlamys smithi: Mauritius;
Chlamys corymbiatus: Hope Islands, northern Queensland, 9-18m;
Pecten (Aequipecten) kikaiensis: Japan, Kikai Island, Kamikatetsu, Wan Formation, Late Pleistocene.

Material examined: The type material. RED SEA: El Bilaiyim, 1 v, HUJ 35602; off Elat, 40-49m, 39 v, 5.ix.1966, MO 28582; off Elat, 40-49m, 20 v, 5.ix.1966, MO 28503; off Elat, 60-90m, 4 v, 5.ix.1966, MO 28505; off Elat, 40-50m, 1 spm., 14 v, 6.ix.1966, MO 28501; off Elat, 180m, 2 v, 6.ix.1966, MO 28522; off Elat, 180m, 1 v, 6.ix.1966, MO 28525; off Elat, 215m, 7 v, 6.ix.1966, MO 28527; off Elat, 215m, 13 v, 6.ix.1966, MO 28521; off Elat, 60-80m, 36 v, 7.ix.1966, MO 28502; off Elat, 60-80m, 80 v, 7.ix.1966, MO 28504; Elat, opposite Old Port, 121m, 6 v, 10.ix.1968, MO 28510; Elat, opposite Old Port, 121m, 8 v, 10.ix.1968, MO 28508; Elat, opposite Zarhin Plant., 167m, 21 v, 16.ix.1968, MO 28511; Elat, opposite Zarhin Plant., 167m, 6 v, 16.ix.1968, MO 28509; Elat, opposite New Port, 220m, 1 v, 16.ix.1968, MO 28506; Elat, opposite New Port, 220m, 1 v, 16.ix.1968, MO 28524; Elat, opposite Oil Port, 350m, 2 v, 16.ix.1968, MO 28532; off Mersat Abu Samra, 60m, 1 v, 6.x.1969, MO 28528; off Mersat Abu Samra, 137m, 25 v, 6.x.1969, MO 28512; off Murach, 91m, 1 v, 6.x.1969, MO 28530; off Nuweiba el Tarabin, 150m, ca. 200 v., 8.x.1969, MO 28500; off Far'un, 64-73m, 1 v, 9.x.1969, MO 28514; off Far'un, 64-73m, 2 v, 9.x.1969, MO 28507; off Wadi Murach, 64-73m, 9 spms., 9.x.1969, NS 16 471; off Wadi Murach, 64-73m, 5 spms., 9.x.1969, NS 16 469; off Marsat Abu Samra, 140m, 1 v, 9.x.1969, MO 28515; off Elat, 242m, 1 v, 17.xi.1969, MO 28523; Gesirath Farun, 64-73m, 1 spm., 9.x.1969, NS 16 472; Elat, opposite Electric Plant., 320m, 1 v, 9.II.1970, MO 28529; Elat, opposite Electric Plant., 320m, 1 v (juv.), 9.II.1970, MO 28518; Elat, opposite Electric Plant., 320m, 1 v, 9.II.1970, MO 28526; Elat, opposite New Port, 270m, 7 v, 13.II.1970, MO 28513; Elat, New Port, 170-270m, 7 v, 13.II.1970, MO 28516; Elat, opposite Old Port, 300-420m, 1 v, 13.ii.1970, MO 28517; Elat, opposite New Port, 170-270m, 7 v, 13.ii.1970, MO 28519; Elat, opposite New Port, 270m, 3 v, 13.ii.1970, MO 28520; Elat, opposite Old Port, 300-420m, 2 v, 13.ii.1970, MO 28531; Gulf of Aqaba, 410m, several v, HUJ 705; Elat, 300m, several v, HUJ 20691; Gulf of Aqaba, 192m, 2 v + 2 fragments; Elat, 280-300m, 1 lv + 5 rv, HUJ 21496; Elat, 70m, 2 lv, HUJ 21497; Gulf of Aqaba, 3 v, HUJ 35591; Gulf of Aqaba, 30-35m, 1 v, HUJ 35595; Elat, harbour, 3 v, HUJ 35605.

Distribution: Red Sea, east coast of Africa to South Africa, Réunion, Mauritius, Arabian Gulf, extending eastwards to southern Japan and New Caledonia. Littoral to bathyal depths, usually sublittoral, living among coral rubble on soft sediments (sand or muddy sand). For more detailed information on distribution and geographical variation see Hayami (1984: 99, 102).

Remarks: Specimens of *C. nux* from the Red Sea are identical in morphological characters to the type specimens. For description of the present species see Hayami (1984: 101) and Dijkstra (1991b: 37). For more information and a comparison with related species see Hayami (1984: 102).

General remarks

The material studied includes 5 taxa new to the Red Sea and adjacent waters: *Delectopecten musorstomi* Poutiers, 1981, *Glorichlamys quadrilirata* (Lischke, 1870), *Gloripallium pallium* (Linnaeus, 1758), *Mirapecten yaroni* n. sp., and *Mimachlamys andamanica* (Preston, 1908).

Oliver (1992) recorded 23 taxa from the area; 6 of which were not present in the material studied: *Propeamussium steindachneri* (Sturany, 1901), *Propeamussium watsoni* (Smith, 1885), *Mimachlamys varia* (Linnaeus, 1758) (identification is doubtful), *Mimachlamys townsendi* (G.B. Sowerby 3rd, 1895), *Volachlamys fultoni* (G.B. Sowerby 3rd, 1904), and *Scaeochlamys livida* (Lamarck, 1819). Thus 27 (or 28) taxa of Pectinoidea are now known from the Red Sea.

The majority of the specimens examined for this work consist of single valves. However, with the exception of *Delectopecten musorstomi*, all species of Pectinidae were represented by live specimen(s) and/or united pair(s) of valves (Table 2).

The geographical distributions of these Red Sea taxa indicate that the following 3 distributional patterns may be distinguished:

1) Distribution extending from the east coast of Africa eastwards into the western Pacific with most taxa having been recorded from New Caledonia and Japan, e.g.

Delectopecten musorstomi Poutiers
Decatopecten plica (Linnaeus)
Excellichlamys spectabilis (Reeve)
Glorichlamys quadrilirata (Lischke)
Gloripallium pallium (Linnaeus)
Juxtamusium maldivense (Smith)
Coralichlamys madreporarum (G.B. Sowerby 2nd)
Pedum spondyloideum (Gmelin)
Mimachlamys andamanica (Preston)
Mimachlamys senatoria (Gmelin)
Cryptopecten nux (Reeve)

2) Distribution restricted mainly to the Indian Ocean, including Mauritius, Réunion, but extending to Indonesia and the Philippines, e.g.

Similipecten eous (Melvill)
Decatopecten amiculum (Philippi)
Laevichlamys rubromaculata (G.B. Sowerby 2nd)
Semipallium crouchi (Smith)

3) Distribution restricted to the Red Sea and adjacent seas. The taxa may constitute an element of an Erythrean zoogeographic subregion, e.g.

Parvamussium formosum (Melvill)
Parvamussium siebenrocki (Sturany)
Parvamussium thyrideum (Melvill)
Gloripallium maculosum (Forsskål)
Mirapecten yaroni n. sp.
Pecten erythraeensis G.B. Sowerby 2nd
Laevichlamys superficialis (Forsskål)

With the exception of *Decatopecten amiculum* (3 samples in the Gulf of Aden

and the southernmost part of the Red Sea) all taxa are recorded from the Gulf of Aqaba and/or the Gulf of Suez. *Mimachlamys senatoria* has not been recorded from the Gulf of Aqaba but occurs in the Gulf of Suez and has also been recorded from the Small Bitter Lake (Suez Canal). *Laevichlamys superficialis* and *Mimachlamys senatoria* are recorded from the Small Bitter Lake (Suez Canal). None of the Red Sea Pectinoidea appear to have migrated into the Mediterranean Sea.

Bathymetric distribution

In the Red Sea, Propeamussiidae have been obtained from 30-35m depth down to 740m (the deepest hauls made). Although more than 1600 valves of the 4 Propeamussiidae species were studied, not a single "live specimen" or united pair of valves was found. The precise habitat of Propeamussiidae in the Red Sea is thus unknown.

The Pectinidae are largely restricted to depths shallower than 40m and 14 taxa of the family have been found as living specimens or united pairs of valves at depths between 0 and 10m. Only one species: *Cryptopecten nux* seems to be restricted to deeper water (40-50m to 64-73m). Dijkstra (1991b) recorded 20 samples of *C. nux* from the Indonesian Archipelago. Valves were obtained there from depths between 37m and 465m and live taken specimens (3 samples) were obtained at 58-80m. These records indicate that *C. nux* is a sublittoral species. Knudsen (1967) recorded live specimens of the attached *Mimachlamys andamanica* from 2000m depth in the Gulf of Aden.

Habitat and mode of life

The Propeamussiidae, so far examined, are predators. The food consists of Foraminifera, minute crustaceans, and larval bivalves (Waller, 1984; Hicks & Marshall, 1985; Morton & Thurston, 1989).

Waller (1984) stated that the ecological range of the Propeamussiidae is nearly as great as that of the Pectinidae. Most propeamussiids live at depths greater than 150m. Most species have a persistent byssal notch and are therefore probably byssate. Morton & Thurston (1989) studied the functional morphology of the bathyal *Propeamussium lucidum* and reported the presence of a byssal notch and the absence of a ctenolium. Bruce Marshall (pers. comm.) observed that living specimens of a propeamussiid (*Cyclochlamys* sp., from Noumea, New Caledonia) "crawled about relatively rapidly on a long, narrow foot, and on reaching a fragment of coral or shell, attached themselves with a single byssal thread, which they pulled up against for orientation. The valves and mantle were then held partly open to reveal the withdrawn foot constantly wriggling within, mimicing a worm to attract prey".

The present 4 species of Red Sea Propeamussiidae have small byssal notches, persisting into adult life (see also Oliver 1992).

The following 11 Red Sea Pectinidae species have been recorded as being byssally attached to corals or stones. The remaining taxa typically live freely in unconsolidated sediment, often under coral blocks or stones:

Excellichlamys spectabilis (Reeve)
Gloripallium pallium (Linnaeus)

Juxtamusium maldivense (Smith)
Mirapecten yaroni n. sp.
Coralichlamys madreporarum (Sowerby 2nd)
Laevichlamys rubromaculata (Sowerby 2nd)
Laevichlamys superficialis (Forsskąl)
Pedum spondyloideum (Gmelin)
Semipallium crouchi (Smith)
Mimachlamys andamanica (Preston)
Mimachlamys senatoria (Gmelin)

Dijkstra (1991b) stated that 90 species of Pectinoidea are known from the Indonesian Archipelago and that this is about 80 % of the known Indo-West Pacific taxa. The 27 (28) species hitherto recorded from the Red Sea indicate a rather low diversity. From the fact that the present survey had added 7 species hitherto unrecorded from the area and the fact that 9 out of 22 species are represented by 6 samples or less, it may be concluded that future investigations will probably increase the number of taxa of Pectinoidea extant in the Red Sea.

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References

Abbott, R. T. 1954. *American seashells.* (Van Nostrand, New York), xiv + 541 pp.

Abbott, R. T. & Dance, S. P. 1982. *Compendium of seashells.* (Dutton, New York),ix + 411pp.

Adam, W. & Leloup, E. 1939. Gastropoda-Pulmonata, Scaphopoda et Bivalvia, *in:* Résultats scientifiques du voyage aux Indes orientales Néerlandaises. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique, Hors série,* **2(20):** 1-126.

Adams, A. & Reeve, L. A. 1850. Mollusca, *in: 'The zoology of the voyage of H. M. S. 'Samarang'; under the command of Captain Sir Edward Belcher, [...] during the years 1843-1846'.* Number 3. Adams, A. (ed.), (Reeve, Benham & Reeve, London), x + 87 pp.

Anthony, M. R. 1906. Liste des mollusques acéphales du Golfe de Tadjourah (Mission Ch. Gravier, 1904). *Bulletin du Muséum d'Histoire Naturelle, Paris* **11:** 490-500.

Appelius, F. L. 1873. Observazioni bibliografiche sui molluschi del Mar Rosso. *Bollettino Malacologico Italiano* **6:** 12-24.

Audouin, V. 1826. Explication sommaire des planches de mollusques de l'Egypte et de la Syrie publiées par J.C. Savigny. Description de l'Egypte ou recueil des observations et des recherches qui ont été faites en Egypte pendant l'expédition de l'armée française, publié par les ordres de sa majesté l'empereur Napoléon le grand. *Histoire naturelle, animaux invertébrés*, Vol. **1(4)**. (Imprimerie impériale, Paris), pp. 7-56.

Audouin, V. [1828] [2nd edition]. *Ibid*, dédiée au roi (1827), Vol. **22**. (Panckouke, Paris), pp. 117-212.

Azuma, M. 1960. *A catalogue of the shell-bearing Mollusca of Okinoshima, Kashiwajima and the adjacent area (Tosa Province)*. (Shikoku, Japan), 102 pp.

Barash, A. & Danin, Z. 1972. The Indo-Pacific species of Mollusca in the Mediterranean and notes on a collection from the Suez Canal. *Israel Journal of Zoology* **21:** 301-374.

Barnard, K. H. 1964. Contributions to the knowledge of South African marine Mollusca, Part 5. Lamellibranchiata. *Annals of the South African Museum* **47(3):** 361-593.

Bavay, A. 1903. Note sur quelques espèces du genre *Pecten*, nouvelles ou mal connues. *Journal de Conchyliologie* **50:** 399-406.

Bavay, A. [1905]. Espèces nouvelles du genre *Pecten* provenant de "l'Indian Museum de Calcutta". *Mémoires de la Société Zoologique de France, Paris* 1904, **17:** 186-190.

Bernard, F. R., Cai, Y. Y. & Morton, B. 1993. *Catalogue of the living marine bivalve molluscs*. (Hong Kong University Press, Hong Kong), 146 pp.

Bosc d'Antic, L. A. G., 1824 [2nd edition]. Histoire naturelle des coquilles, [...], Vol. 2. (Verdière, Paris), 326 pp.

Bosch, D. & Bosch, E. 1982. *Seashells of Oman*. (Longman, London and New York), 206 pp.

Bosch, D. T., Dance, S. P., Moolenbeek, R. G. & Oliver, P. G. 1995. *Seashells of Eastern Arabia*. (Motivate, Dubai, Abu Dhabi and London), 296 pp.

Bouchet, P. & Danrigal, F. 1982. Napoleon's Egyptian campaign (1798-1801) and the Savigny collection of shells. *Nautilus* **96(1):** 9-24.

Bronn, H. G. 1832. Ergebnisse meiner naturhistorisch-öconomischen Reisen, Vol. 2. *Skizzen und Ausarbeitungen über Italien nach einem zweyten Besuche im Jahre 1827*. (Heidelberg, Leipzig), xviii + 686 pp.

Cahill, M. 1979. *Pecten. Mirapecten* update. *Shell Collector* **2:** 28-[30], [35]-37.

Catlow, A. & Reeve, L. A. 1845. The conchologist's nomenclator. *A catalogue of the recent species of shells, included under the sub-kingdom 'Mollusca'*, [...]. (Reeve, London), viii + 326 pp.

Chemnitz, J. H. 1784. *Neues systematisches Conchylien-Cabinet* [...], Band 7.(Raspe, Nürnberg), 356 pp.

Chemnitz, J. H. 1785. *Neues systematisches Conchylien-Calinet* [...], Band 8. (Raspe, Nürnberg), 372 pp.

Chemnitz, J. H. 1795. *Neues systematisches Conchylien-Cabinet* [...], Band 11. (Raspe, Nürnberg), 310 pp, pls 174-213.

Chenu, J. C. 1842-54. *Illustrations conchyliologiques ou descriptions et figures de toutes les coquilles connues vivants et fossiles, classées suivant le système de Lamarck*. (Fortin & Masson, Langlois & Leclercq, Paris), 482 pls.

Chenu, J. C. 1862. *Manuel de Conchyliologie et de Paléontologie conchyliologique*, Vol. 2. (Masson, Paris), 329 pp.

Cooke, A. H. 1886. On Testaceous Mollusca obtained in the Gulf of Suez. *Annals and Magazine of Natural History* **17:** 134-135.

Cotton, B. C. 1964. Molluscs of Arnhem Land, *in*: 'Records of the American-Australian scientific expedition to Arnhem Land', Vol. 4, Zoology. Specht, R.L. (ed.), (Melbourne University Press, Melbourne), pp. 9-44.

Cox, L. R. 1929. Notes on the Post-Miocene Ostreidae and Pectinidae of the Red Sea region, with remarks on the geological significance of their distribution. *Proceedings of the Malacological Society of London* **18:** 175-209.

Cox, L. R. 1930. Reports on geological collections from the coastlands of Kenya Colony made by Miss M. McKinnon Wood, V: Miocene Mollusca. VI: Pliocene Mollusca. VII: Post-Pliocene Mollusca. *Monographs of the Geological Department of the Hunterian Museum, Glasgow University* **4:** 103-163.

Crandall, P. R. 1979. A new *Chlamys* from the Ryukyu Islands, Japan. *Quaterly Journal of the Taiwan Museum* **32(1-2):** 114-115.

Da Costa, E. M. 1778. *Historia naturalis testaceorum Britanniae, or the British Conchology, containing the natural history of the shells of Great Britain and Ireland in English and French.* (White, Elmsley & Robson, London), xii + 254 + x pp.

Dall, W. H., Bartsch, P. & Rehder, H. A. 1938. A manual of the Recent and fossil marine pelecypod mollusks of the Hawaiian Islands. *Bernice P. Bishop Museum Bulletin* **153:** 1-233.

Dance, S. P. 1974. *The encyclopedia of shells.* (Blandford Press, London), 288 pp.

Dance, S. P. 1986. *A history of shell collecting.* (Brill & Backhuys, Leiden), xv + 265 pp.

Dautzenberg, P. & Bavay, A. 1912. Les lamellibranches de l'expédition du 'Siboga'. Systématique. I. Pectinidés. *Siboga-Expeditie Monographie* **53b:** 1-41.

Dautzenberg, P. & Bouge, J. L. 1933. Les mollusques testacés marins des établissements Français de l'Océanie. *Journal de Conchyliologie* **77:** 426-428.

Dautzenberg, P. 1929. Mollusques testacés marins de Madagascar. *Faune des Colonies Françaises* **3:** 321-636.

Deshayes, G. P. 1830. Coquilles de la Mer Rouge, *in*: 'Voyage de l'Arabie Pétrée', 1830-34. Laborde, L. E. S. J. de and Linant, (Giard, Paris), p. 66.

Deshayes, G. P. 1836 [2nd edition]. Peigne (Pecten), *in*: Histoire naturelle des animaux sans vertèbres, [...], Vol. 7. Histoire des Mollusques, Lamarck, J. P. B. A. de M. de, (Baillière, Paris), pp. 128-174.

Deshayes, G. P. 1863. Catalogue des mollusques de l'Île de la Réunion (Bourbon), *in*: 'Notes sur l'Île de Réunion (Bourbon)', Part 2, Annexe E. Maillard, L., (Dentu, Paris), 144 pp.

Dijkstra, H. H. 1984a. Rare or poorly known pectinids, Part 3. *La Conchiglia /The Shell* **16(182-3):** 3-5.

Dijkstra, H. H. 1984b. Rare or poorly known pectinids, Part 5. *La Conchiglia /The Shell* **16(186-7):** 8-9.

Dijkstra, H. H. 1984c. Les Pectinidae de N. Calédonie. The Pectinidae of NewCaledonia, Part 6. *Gloripallium pallium* (Linnaeus, 1758). *Rossiniana* **(25):** 17-18.

Dijkstra, H. H. 1986a. Les Pectinidae de N. Calédonie. The Pectinidae of New Caledonia, Part 11. *Chlamys perfecta* (Melvill, 1909). *Rossiniana* **(31):** 9.

Dijkstra, H. H. 1986b. Les Pectinidae de N. Calédonie. The Pectinidae of New Caledonia, Part 12. *Chlamys (Coralichlamys) madreporarum* ([Petit in] Sowerby II, 1842). *Rossiniana* **(32):** 7-8.

Dijkstra, H. H. 1987a. Les Pectinidae de N. Calédonie. The Pectinidae of New Caledonia, Part 13. *Excellichlamys spectabilis* (Reeve, 1853). *Rossiniana* **(35):** 9-10.

Dijkstra, H. H. 1987b. Les Pectinidae de N. Calédonie. The Pectinidae of NewCaledonia, Part 14. *Pedum spondyloideum* (Gmelin, 1791). *Rossiniana* **(36):** 9-10.

Dijkstra, H. H. 1988a. *Mirapecten moluccensis* sp. n. from the Moluccas. *La Conchiglia /The Shell* **20(234-5):** 12-14.

Dijkstra, H. H. 1988b. Les Pectinidae de Nouvelle-Calédonie. The Pectinidae of New Caledonia, Part 19. *Cryptopecten bernardi* fa.*corymbiatus* (Hedley, 1909). *Rossiniana* **(41):** 7-8.

Dijkstra, H. H. 1989. Rare or poorly known pectinids, part 10. *La Conchiglia / The Shell* **21(242-5):** 12-15.

Dijkstra, H. H. 1990. Pectinides des fonds meubles dans les lagons de N. Calédonie et de Chesterfield. Pectinidae found on the soft bottoms of the New Caledonian and Chesterfield lagoons. *Rossiniana* **(46):** 3-10.

Dijkstra, H. H. 1991a. Les Pectinidae de N. Calédonie / The Pectinidae of New Caledonia. *Rossiniana* **(50):** 22-23.

Dijkstra, H. H. 1991b. A contribution to the knowledge of the pectinacean Mollusca (Bivalvia: Propeamussiidae, Entoliidae, Pectinidae) from the Indonesian Archipelago. *Zoologische Verhandelingen, Leiden* **(271):** 1-57.

Dijkstra, H. H. 1993. Les Pectinidae de Nouvelle Calédonie. The Pectinidae of New Caledonia. *Rossiniana* **(56):** 10-11.

Dijkstra, H. H. 1994. Type specimens of Recent species of Pectinidae described by Lamarck (1819), preserved in the Muséum d'Histoire Naturelle of Geneva and the Muséum National d'Histoire Naturelle of Paris. *Revue Suisse de Zoologie* **101(2):** 465-532.

Dijkstra, H. H. 1995. Bathyal Pectinoidea (Bivalvia: Propeamussiidae, Entoliidae, Pectinidae) from New Caledonia and adjacent areas, *in*: Résultats des Campagnes MUSORSTOM, Vol. 14. Bouchet, P. (ed.). *Mémoires du Muséum national d'Histoire naturelle, Zoologie* **167:** 9-73.

Dijkstra, H. H. 1997. Results of the Rumphius Biohistorical Expedition to Ambon (1990) Part 6. Mollusca, Bivalvia, Pectinidae. *Zoologische Mededelingen, Leiden* **71(27):** 313-343.

Dijkstra, H. H. [in press]. Type specimens of Pectinidae (Mollusca: Bivalvia) described by Linnaeus (1758-1771). *Zoological Journal of the Linnean Society.*

Dijkstra, H. H. & Kastoro, W. W. 1997. Mollusca Bivalvia: Pectinoidea (Propeamussiidae and Pectinidae) from eastern Indonesia, *in*: Résultats des Campagnes MUSORSTOM, Vol. 16. Crosnier, A. & Bouchet, P. (eds). *Mémoires du Muséum national d'Histoire naturelle, Zoologie* **172:** 245-285.

Dijkstra, H. H. & Kilburn, R. N. [in prep.]. The family Pectinidae in southern Africa and Mozambique (Mollusca, Bivalvia, Pectinoidea). *Annals of the Natal Museum.*

Dijkstra, H. H. & Marshall, B. A. 1997. Pectinoidea (Mollusca: Bivalvia: Propeamussiidae: Pectinidae) of Lord Howe Island, Norfolk Island and the Kermadec Islands. *Molluscan Research* **18:** 73-114.

Dijkstra, H. H., Richer de Forges, B., Clavier, J. & Lefort, Y. 1989-90. Pectinidés des fonds meubles dans les lagons de N. Calédonie et de Chesterfield. Pectinidae found on the soft bottoms of the New Caledonian and Chesterfield lagoons. *Rossiniana* **45:** 21-24 (Part 1); *Rossiniana* **46:** 3-10 (Part 2); *Rossiniana* **47:** 3-9 (Part 3).

Dillwyn, L. W. 1817. *A descriptive catalogue of Recent shells, arranged according to the Linnaean method; with particular attention to the synonymy.* (J. & A. Arch, London), xii + 1092 + [29] pp.

Dodge, H. 1952. A historical review of the mollusks of Linnaeus, Part 1. *Bulletin of the American Museum of Natural History* **100:** 1-263.

Dunker, W. B. R. H. 1864. Fünf neue Mollusken. *Malakozoologische Blätter* **11:** 99-102.

Dunker, W. B. R. H. 1877. Mollusca nonnulla nova maris Japonici. *Malakozoologische Blätter* **24:** 67-75.

Dunker, W. B. R. H. 1882. *Index molluscorum maris Japonici* [...]. (Fischer, Cassel), vii + 301 pp.

Eames, F. E. & Cox, L. R. 1956-57. Some Tertiary Pectinacea from East Africa, Persia, and the Mediterranean region. *Proceedings of the Malacological Society of London* **32:** 1-68.

Eichwald, C. E. von 1830. *Naturhistorische Skizze von Lithauen, Volhynien und Podolien in geognostisch-mineralogischer, botanischer und zoologischer Hinsicht entworfen.* (Von Eichwald, Wilna), 256 pp.

Favanne de Montcervelle de, J. & G. J. de 1780 [3rd edition]. *La conchyliologie, avec un traité de zoomorphose.* (De Buré, Paris), lx + 878 + 848 pp., 80 pls.

Finlay, H. J. 1926. A further commentary on New Zealand molluscan systematics. *Transactions and Proceedings of the New Zealand Institute* **57:** 320-485.

Fischer, P. 1858. Notes pour servir à la faune malacologique de l'Archipel Calédonien. *Journal de Conchyliologie* **7:** 329-342.

Fischer, P. 1865. Note sur les faunes conchyliologiques de deux rivages de l'isthme de Suez. *Journal de Conchyliologie* **13:** 241-248.

Fischer, P. 1870. Sur la faune conchyliologiques marine des Baies de Suez et de l'Akabah. *Journal de Conchyliologie* **18:** 161-179.

Fischer, P. 1871. Sur la faune conchyliologique marine de Suez. *Journal de Conchyliologie* **19:** 209-226.

Fleming, C. A. 1957. The genus *Pecten* in New Zealand. *New Zealand Geological Survey Paleontological Bulletin* **26:** 1-69.

For[s]skąl, P. 1775. *Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit Petrus Forskąl. Prof. Haun. Post mortem auctoris edidit Carsten Niebuhr.* (Møller, Copenhagen), xxxiv + 140 pp. [Preface by Biebuhr, 19 pp].

Franc, A. 1956. Résultats scientifiques des campagnes de la "Calypso" 2. Campagne 1951-52 en Mer Rouge. IX. Mollusques marins. *Annales de l'Institut Océanographique, Monaco,* N.S., **23:** 19-60.

Glayzer, B. A., Glayzer, D. T. & Smythe, K. R. 1984. The marine mollusca of Kuwait, Arabian Gulf. *Journal of Conchology* **31:** 311-330.

Gmelin, J. F. 1791. Caroli a Linné, systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 13th edition, Aucta, Reformata, Vol. **1 (6).** (Beer, Lipsiae), pp. 3021-3909.

Gould, A. A. 1850. The shells from the United States Exploring Expedition. *Proceedings of the Boston Society of Natural History* **3:** 275-278, 309-312, 343-348.

Grau, G. 1959. Pectinidae of the eastern Pacific. *Allan Hancock Pacific Expeditions,* Vol. **23.** (University of Southern California Publ., Los Angeles), viii + 308 pp.

Gray, J. E. 1847. A list of the genera of Recent mollusca, their synonyma and types. *Proceedings of the Zoological Society of London* **15:** 129-206.

Habe, T. 1951. Genera of Japanese shells. Pelecypoda, No. 1. (Kairui-Bunken-Kankokai, Tokyo), 96 pp. [In Japanese]

Habe, T. 1961. *Colored illustrations of the shells of Japan,* Vol. **2.** (Hoikusha, Osaka), 223 pp. [In Japanese]

Habe, T. 1964. *Shells of the Western Pacific in color,* Vol. **2.** (Hoikusha, Osaka), 223 pp.

Habe, T. 1977. *Systematics of Mollusca in Japan. Bivalvia and Scaphopoda.* (Hokuryukan, Tokyo), 372 pp. [In Japanese]

Hall, W. J. & Standen, R. 1907. On the Mollusca of a raised coral reef on the Red Sea coast. *Journal of Conchology* **12(3):** 65-68.

Hanley, S. P. 1842-56. An illustrated and descriptive catalogue of Recent bivalve shells. (Williams & Norgate, London), xviii + 392 + 24 pp.

Hanley, S. P. 1855. Ipsa Linnaei Conchylia. *The shells of Linnaeus, determined from his manuscripts and collections.* (Williams & Norgate, London), 556 pp.

Hayami, I. 1982. Taxonomic names of *Cryptopecten* species. *Venus* **41(3):** 233-236.

Hayami, I. 1984. Natural history and evolution of *Cryptopecten* (A Cenozoic-Recent pectinid genus). *Bulletin of the University Museum of Tokyo* **24:** 1-149.

Hayami, I. 1989. Outlook on the Post-Paleozoic historical biogeography of pectinids in the Western Pacific region, *in*: 'Current aspects of biogeography in West Pacific and East Asian regions. Nature and Culture 1'. Ohba, H., Hayami, I. & Mochizuki, K. (eds), (University Museum, University of Tokyo, Tokyo), pp. 3-25.

Hedley, C. 1909. Mollusca from the Hope Islands, North Queensland. *Proceedings of the Linnean Society of New South Wales* **34:** 420-466.

Herrmannsen, A. N. 1846-49. Indicis generum malacozoorum primordia [...]. Praetermittuntur Cirripedia, Tunicata et Rhizopoda. (Fischer, Casselis), Vol. 1, 1846-47, 637 pp.; Vol. 2, 1847-49, 717 pp.

Hertlein, L. G. 1969. Family Pectinidae Rafinesque, 1815, *in*: 'Treatise on invertebrate paleontology', Part N, Vol. 1 (of 3), pp. N348-372. Mollusca 6, Bivalvia. Moore, R.C. (ed.), (Geological Society of America and University of Kansas, Lawrence).

Hicks, G. R. F. & Marshall, B. A. 1985. Sex selective predation of deep-sea, meiobenthic copepods by pectinacean bivalves and its influence on copepod sex ratios. *New Zealand Journal of Marine and Freshwater Research* **19:** 227-231.

Hidalgo, J. G. 1904-05. Catalogo de los moluscos testáceos de las Islas Filipinas, Joló y Marianas. 1 Moluscos Marinos. Revista de la R. Academia de Ciencias Exactas Fisicas y Naturales de Madrid 1-3: i-xvi, 1-408.

Hinds, R. B. 1844-45. The zoology of the voyage of H.M.S. "Sulphur", under the command of Capt. Sir E. Belcher, during 1836-1843. *Mollusca,* Part 3. (Smith & Elder, London), 72 pp.

Horning, A. & Mermod, G. 1928. Mollusques de la Mer Rouge recueillis par A. Issel faisant partie des collections du Musée Civique d'Histoire Naturelle de Genèves. *Annali del Museo Civico di Storia Naturale Giacomo Doria di Genova* **52:** 20-33, 202-209, 363-372; *ibid.* **53:** 108-121.

Iredale, T. 1929. Mollusca from the continental shelf of eastern Australia, No. 2. *Records of the Australian Museum* **17(4):** 157-189.

Iredale, T. 1939. Mollusca, Part 1, *in*: 'B. M. (N. H.) Great Barrier Reef Expedition 1928-29'. Sciences Reports, Vol. 5(6). (British Museum Natural History, London), pp. 209-425.

Issel, A. 1869. *Malacologia del Mar Rosso. Ricerche zoologiche e paleontologiche.* (Biblioteca malacologica, Pisa), xi + 387 pp.

Jousseaume, F. 1886. Coquilles marines des côtes d'Abyssinie et de Zanzibar recueillies par M. Raffray en 1873 et en 1874. *La Naturaliste* **7(1):** 220-222.

Jousseaume, F. 1888. Description des mollusques recueillis par M. le Dr. Faurot dans la mer Rouge et le Golfe d'Aden. *Mémoires de la Société Zoologique de France* **1(2):** 165-223.

Kilburn, R. N. & Dijkstra, H. H. 1995. A new species of *Pecten* Müller, 1776, from South Africa, with a note on '*Pecten sulcicostatus* var. *casa*' van Bruggen, 1961 (Mollusca: Bivalvia: Pectinidae). *Annals of the Natal Museum* **36:** 271-279.

Kira, T. 1962. *Shells of the Western Pacific in color.* (Hoikusha, Osaka), 224 pp.

Kira, T. 1967 [3rd edition]. *Shells of the Western Pacific in color.* (Hoikusha, Osaka), 224 pp.

Kleemann, K. 1990. Coral associations, biocorrosion, and space competition in *Pedum spondyloideum* (Gmelin) (Pectinacea, Bivalvia). *Marine Ecology* **11(1):** 77-94.

Klein, J. T. 1753. *Tentamen methodi ostracologicae, sive dispositio naturalis [...] cochlidum et concharum.* (Wishoff, Lugduni Batavorum [Leiden]), viii + 177pp.

Knudsen, J. 1967. The deep-sea Bivalvia. John Murray Exped., Vol. 11(3). *Publications of the British Museum (Natural History)* **(657):** 239-343.

Koch, F. C. L. & Dunker, W. B. R. H. 1837. *Beiträge zur Kenntniss des Norddeutschen Oolithgebildes und dessen Versteinerungen.* (Oehme & Müller, Braunschweig), 64 pp.

Küster, H. C. & Kobelt, W. 1842-88. Die Gattungen *Spondylus* und *Pecten*, *in*: 'Systematisches Conchylien-Cabinet von Martini und Chemnitz', Vol. **7(2).** (Bauer & Raspe, Nürnberg), pp. 1-129.

Kuroda, T. 1929-35. An illustrated catalogue of the Japanese shells, Parts 1-16. *Venus* **1-5:** 1-154, appendices. [In Japanese]

Kuroda, T., Habe, T. & Oyama, K. 1971. *The sea shells of Sagami Bay collected by His Majesty the Emperor of Japan.* (Maruzen, Tokyo), 741 + 487 pp.

Lamarck, J. B. P. A. de M. de 1799. Prodome d'une nouvelle classification des coquilles. *Mémoire de la Société Histoire naturelle, Paris* **1:** 63-91.

Lamarck, J. B. P. A. de M. de 1819. *Histoire naturelle des animaux sans vertèbres,* [...], Vol. **6(1).** (Author, Paris), 343 pp.

Lamprell, K. & Whitehead, T. 1992. *Bivalves of Australia,* Vol. **1.** (Crawford House Press, Bathurst), xiii + 182 pp.

Lamy, E. 1928. Les Peignes de la Mer Rouge (d'après les matériaux recueillis par le Dr Jousseaume). *Bulletin du Muséum National d'Histoire Naturelle* **34:** 166-172, 219-220.

Lamy, E. 1935. Catalogue des Pectinidae vivants du Muséum National d'Histoire Naturelle de Paris déterminés par feu A. Bavay. *Journal de Conchyliologie* **79:** 306-321.

Lamy, E. 1938. Mission Robert Ph. Dollfus en Egypte. VII. Mollusca testacea. *Mémoires de l'Institute d'Egypte* **37:** 1-89.

Laskey, J. 1811. Account of North British Testacea. *Memoirs of the Wernerian Natural History Society, Edinburgh* **1:** 370-417.

Liénard, E. 1877. *Catalogue de la faune malacologique de l'Ile Maurice et de ses dépendances comprenant les Iles Seychelles, le groupe de Chagos composé de Diego-Garcia, Six-Iles, Peros-Banhos, Salomon, etc., l'Iles Rodrigues, l'Ile de Cargados ou Saint-Brandon.* (Savy, Paris), iv + 115 pp.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae* [...] Editio decima, reformata, Vol. **1.** Regnum animale. (Salvii, Holmiae [Stockholm]), iii + 824 pp.

Linnaeus, C. 1764. *Museum S:ae R:ae M:tis Ludovicae Ulricae Reginae Svecorum, Gothorum, Vandalorumque* [...]. (Salvii, Holmiae [Stockholm]), 110 pp.

Linnaeus, C. 1766-67. *Systema naturae per regna tria naturae* [...]. Editio Duodecima Reformata. Regnum Animale. (Salvii, Holmiae [Stockholm]), 1327 pp.

Lischke, C. E. 1870. Diagnosen neuer Meeres-Conchylien von Japan. *Malakozoologische Blätter* **17:** 23-29.

Lischke, C. E. 1871. *Japanische Meeres-Conchylien.* Ein Beitrag zur Kenntniss der Mollusken Japan's mit besonderer Rücksicht auf die geographische Verbreitung derselben, Vol. **2.** (Fischer, Cassel), 184 pp.

Lynge, H. 1909. The Danish Expedition to Siam 1899-1900. IV. Marine Lamellibranchiata. *Kongelige Danske Videnskabernes Selskabs Skrifter, Kjøbenhavn* **5(7):** 100-299.

Macandrew, R. 1870. Report on the testaceous Mollusca obtained during the dredging excursion in the Gulf of Suez in the months Febr. and March, 1869. *Annals and Magazine of Natural History,* **4e Ser., 6:** 429-450.

Martens, E. von 1880. Mollusken, *in*:'Beitrage zur Meeresfauna der Insel Mauritius und der Seychellen bearbeitet von K. Möbius, F. Richters und E. von Martens nach Sammlungen, angelegt auf einer Reise nach Mauritius', [...]. Möbius, K. A. (ed.), (Gutmann, Berlin), pp. 179-336, 346-352.

Mastaller, M. 1978. The marine molluscan assemblages of Port Sudan, Red Sea. *Zoologische Mededelingen, Leiden* **53(13):** 117-144.

Mastaller, M. 1979. *Beiträge zur Faunistik und Ökologie der Mollusken und Echinodermen in den Korallenriffen bei Aqaba, Rotes Meer.* (Gräbner, Altendorf), 344 pp.

Mastaller, M. 1987. Molluscs of the Red Sea, *in*:'Red Sea'. Edwards, A. J. & Head, S. M. (eds), (Pergamon Press, Oxford, etc.), pp. 194-214.

Melvill, J. C. 1888. Descriptions of six new species of Pecten. *Journal of Conchology* **5:** 279-281.

Melvill, J. C. 1909. Report on the marine Mollusca obtained by Mr. J. Stanley Gardiner F. R. S., among the Islands of the Indian Ocean in 1905. *Transactions of the Linnean Society of London*, Ser. **2**, *Zoology* **13:** 65-138.

Melvill, J. C. & Standen, R. [1907]. The Mollusca of the Persian Gulf, Gulf of Oman and Arabian Sea as evidenced mainly through the collections of Mr. F.W. Townsend, 1893-1906, with descriptions of new species, Part 2. Pelecypoda. *Proceedings of the Zoological Society of London 1906*, **54:** 783-848.

Mergner, H. 1979. Quantitative ökologische Analyse eines Rifflagunen-areals bei Aqaba (Golf von Aqaba, Rotes Meer). *Helgoländer wissenschaftliche Meeres-untersuchungen* **32:** 476-507.

Moazzo, P. G. 1939. Mollusques testacés marins du Canal de Suez. *Mémoires de l'Institut d'Egypte* **38:** 1-283.

Mörch, O. A. L. 1853. *Catalogus Conchyliorum quae reliquit D. Alphonso d'Aguirra and Gadea, comes de Yoldi*, [...]. (Höst, Hafniae [Copenhagen]), 32 + 74 pp.

Morton, B. & Thurston, M. H. 1989. The functional morphology of *Propeamussium lucidum* (Bivalvia: Pectinacea), a deep-sea predatory scallop. *Journal of Zoology, London* **218:** 471-496.

Mühlhäusser, H. 1985. Pectinidae from Maldive Islands. *La Conchiglia / The Shell* **17(196-7):** 8-9.

Müller, O. F. 1776. *Zoologiae Danicae prodromus, seu animalium daniae et Norvegiae indigenarum, characteres, nomina, et synonyma imprimis popularium.* (Hallageriis, Havniae [Copenhagen]), xxxii + 282 pp.

Nielsen, C. 1986. Fauna associated with the coral Porites from Phuket, Thailand, Part 1: Bivalves with description of a new species of *Gastrochaena. Phuket Marine Biological Center, Research Bulletin* **42:** 1-24.

Nomura, S. 1933. Catalogue of the Tertiary and Quaternary Mollusca from the Island of Taiwan (Formosa) in the Institute of Geology and Palaeontology, Tohoku Imperial University. *Science Reports of the Tôhoku (Imperial) University, Sendai* **[2] 16:** 1-108.

Nomura, S. & Zinbo, N. 1934. Marine Mollusca from the "Ryukyu Limestone" of Kikaizima, Ryukyu Group. *Science Reports of the Tôhoku (Imperial) University, Sendai* **[2] 16:** 109-164.

Oliver, P. G. 1982. *Handlists of the molluscan collections in the Department of Zoology, National Museum of Wales*, Ser. **1.** The Melvill-Tomlin Collection, Part 11, Pectinacea (Pectinidae). (National Museum of Wales, Cardiff), 17 + xi + vii + ii pp.

Oliver, P. G. 1992. *Bivalved seashells of the Red Sea.* (Christa Hemmen, Wiesbaden, and National Museum of Wales, Cardiff), 330 pp.

Paetel, F. 1890 [4th revised edition]. Die Acephalen und die Brachiopoden. *in*: Catalog der Conchylien-Sammlung von Fr. Paetel. Nebst Übersicht des angewandten Systems, Vol. 3. (Paetel, Berlin), 256 + xxxii pp.

Pagenstecher, H. A. 1877. Zoologische Ergebnisse einer im Auftrage der [...] Academie [...] ausgeführten Reise in die Küstgegenden des Rothen Meeres. [...]. Mollusca, Part 2. (Kossmann, Leipzig), 66 pp.

Pallary, P. 1926. Explication des planches de J.C. Savigny. *Mémoires d'Institute Egypte* **11:** i-viii, 1-138.

Pallary, P. 1932. Inventaire de la collection malacologique de Savigny. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 2e Ser., **4(3):** 313-321.

Petit [de la Saussaye], M. S. 1853. Description d'une variété du *Pecten histrionicus* Gmel. *Journal de Conchyliologie* **4:** 150-152.

Philippi, R. A. 1842-45. *Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien, unter Mithülfe mehrerer deutscher Conchyliologen*, Vol. 1. (Fischer, Cassel), 204 pp.

Philippi, R. A. 1851. Centuria quinta Testaceorum novorum. *Zeitschrift für Malakozoologie* **8(6):** 29-96, 123-126.

Pilsbry, H. A. 1895. *Catalogue of the marine mollusks of Japan with descriptions of new species and notes on others collected by Frederick Stearns.* [...]. (Stearns, Detroit), viii + 196 pp.

Poutiers, J. M., 1981. Mollusques: Bivalves, *in*: 'Résultats des campagnes MUSORSTOM', Vol 1: Philippines (18-28 Mars 1976). *Mémoires du Muséum national d'Histoire naturelle, Zoologie* **91:** 325-356.

Preston, H. B. 1908. Descriptions of new species of land, marine and freshwater shells from the Andaman Islands. *Records of the Indian Museum* **2(2):** 187-210.

Preston, H. B. 1909. Description of new land and marine shells from Ceylon and S. India. *Records of the Indian Museum, Calcutta* **3(2):** 133-140.

Quoy, J. R. C. & Gaimard, J. P. 1835. *Voyage de découvertes de l'Astrolabe exécuté par ordere du Roi, pendant les années 1826-1827-1828-1829, Zoologie*, Vol. **3(2)**. (Tastu, Paris), 712 pp.

Rees, W. J. & Stuckey, A. 1952. The 'Manihine' expedition to the Gulf of Aqaba 1948-49. VI. Mollusca. *Bulletin of the British Museum (Natural History), Zoology* **1(8):** 183-201.

Reeve, L. A. 1841. *Conchologia systematica, or complete system of conchology* [...], Vol. **1.** (Longmans, London), vi + 195 pp.

Reeve, L. A. 1852-53. Monograph of the genus *Pecten*, *in*: 'Conchologia iconica: or, illustrations of the shells of molluscous animals', Vol. **8.** (Reeve, London), pls 1-35.

Reeve, L. A. 1860. Elements of conchology; an introduction to the natural history of shells and of the animals which form them, Vol. **2.** (Reeve, London), vi + 203 pp.

[Röding, P. F.] 1798. *Museum Boltenianum* [...] Pars secunda, continens conchylia sive testacea univalvia, bivalvia et multivalvia. (Trapp, Hamburgi), viii + 199 pp.

Rombouts, A. 1991. *Guidebook to Pecten shells. Recent Pectinidae and Propeamussiidae of the world.* (Universal Book Services / Backhuys, Oegstgeest), xiii + 157 pp.

Ryland, A. T. 1951. The shells of the Suez Canal. *Royal Air Force Educational Branch*: 1-27.

Sacco, F. 1897a. *I molluschi dei terreni terziarii del Piemonte e della Liguria,* Part 23 (Ostreidae, Anomiidae e Dimyidae). *Bollettino dei Musei di zoologia e anatomia comparata della Reale Universita di Torino* **12 (298):** 99-100.

Sacco, F. 1897b. *I molluschi dei terreni terziarii del Piemonte e della Liguria,* Part 24 (Pectinidae). (Carlo Clausen, Torino), pp 3-117.

Savigny, J. C. 1817. Description de l'Egypte, ou recueil des observations et des recherches qui ont été faites en Egypte pendant l'Expédition de l'armée française, [...]. Histoire naturelle, Vol. **2.** (Imprimerie royale, Paris), 752 pp.

Schmidt, F. C. 1818. *Versuch über die beste Einrichtung zur Aufstellung, Behandlung und Aufbewahrung der verschiedenen Naturkörper und Gegenstände der Kunst, verzüglich der conchylien-Sammlungen, nebstkurzer Beurtheilung der conchyologischen Systeme und Schriften.* (Perthes, Gotha), 252 pp.

Schumacher, H. C. F. 1817. *Essai d'un nouveau système de habitations des vers testacés.* (Schultz, Copenhague), iv + 287 pp.

Schröter, J. S. 1802. Neue Conchylienarten und Abänderungen, Anmerkungen und Berichtungen, nach dem Linnéischen System der XIIten Ausgabe, zweite Fortsetzung. *Archiv für Zoologie und Zootomie* **3 (1):** 125-166.

Selli, R. 1973. Molluschi quaternari di Massaua e di Gibuti. *in*: Missione g e o l o g i c a dell'azienda generale Italiana petroli (A.G.I.P.) nella dancalia meridionale e sugli altipiani hararini. *Documentazione Paleontologia* **4(2):** 151-444.

Sganzin, V. 1843. Catalogue des coquilles trouvées aux îles de France, de Bourbon et de Madagascar. *Mémoires de la Société du Muséum d'Histoire Naturelle de Strasbourg, Paris* **3(2):** 1-30.

Sharabati, D. P. 1981. *Saudi Arabian seashells.* (VNU Books International), 119 pp.

Sharabati, D. P. 1984. *Red Sea shells.* (KPI Ltd., London), 127 pp.

Shikama, T. 1964. *Selected shells of the world illustrated in colours,* Vol. **2.** (Hokuryukan, Tokyo), 212 pp. [In Japanese]

Shopland, E. R. 1896. List of shells collected at Aden in 1892-95, classified in accordance with the Paetel catalogue. *Journal of the Bombay Natural History Society* **10(2):** 217-235.

Shopland, E. R. 1902. List of marine shells collected in the neighbourhood Aden between 1892 and 1901. *Proceedings of the Malacological Society of London* **5(2):** 171-179.

Smith, E. A. 1885. Report on the Lamellibranchiata collected by H. M. S. "Challenger" during the years 1873-1876, *in*: 'Report on the scientific results of the voyage of H.M.S. "Challenger" during the years 1873-1876'. Zoology, Vol. **13(35).** (Her Majesty's Government, London), 341 pp.

Smith, E. A. 1891. On a collection of marine shells from Aden. *Proceedings of the Zoological Society of London* **(1891):** 370-436.

Smith, E. A. 1892. Description of new species of shells from Mauritius and California. *Annals and Magazine of Natural History* **(1892):** 255-256.

Smith, E. A. 1903. Marine Mollusca, *in*:'The fauna and geography of the Maldive and Laccadive Archipelagoes', [...], Vol. **2 (2).** Gardiner, J. S. (ed.), (University Press, Cambridge), pp. 589-630..

Smith, E. A. 1904. Natural history from H.M. Indian Marine Survey Steamer "Investigator", commander T.H. Heming, R.N. - Series III, No. 1. On Mollusca from the Bay of Bengal and the Arabian Sea. *Annals and Magazine of Natural History* **13:** 453-473; *ibid.* **14:** 1-14.

Smythe, K. R. 1972. Marine Mollusca from Bahrain Island, Persian Gulf. *Journal of Conchology* **27:** 491-496.

Smythe, K. R. 1979. The marine Mollusca of the United Arab Emirates, Arabian Gulf. *Journal of Conchology* **30:** 57-80.

Soest, R. W. M. van 1994. On the intimate relationships of molluscs and sponges, *in*: 'De horen en zijn echo'. Coomans-Eustatia, M., Moolenbeek, R., Los, W. and Prins, P. (eds), (Stichting Libri Antilliani, Bloemendaal and Zoölogisch Museum Amsterdam, Amsterdam), pp. 71-75.

Sowerby, G. B. 1st 1835. Characters and observations on new genera and species of Mollusca and Conchifera collected by Mr. Cuming. *Proceedings of the Zoological Society of London* **3:** 4-7, 49-51, 93-96, 109-110.

Sowerby, G. B. 2nd 1839. *A conchological manual.* (Sowerby, London), v + 130 pp.

Sowerby, G. B. 2nd 1842. Monograph of the genus *Pecten, in*:'Thesaurus conchyliorum', Vol. **1.** (Sowerby, London), pp. 45-78, pls 12-20.

Sowerby, G. B. 3rd 1895. Descriptions of nine new species of shells. *Proceedings of the Malacological Society of London* **1:** 214-217.

Sowerby, G. B. 3rd 1904. Mollusca of South Africa (Pelecypoda). *Marine Investigations in South Africa* **4:** 1-19.

Sowerby, G. B. 3rd 1908. Descriptions of eight new species of marine Mollusca. *Proceedings of the Malacological Society of London* **8:** 16-19.

Sowerby, J. de C. 1828. *The mineral conchology of Great Britain;* [...], Vol. **6(3).** (Meredith, London), pp. 157-200.

Stearns, F. & Pilsbry, H. A. 1895. *Catalogue of the marine mollusks of Japan.* (Stearns, Detroit), viii + 196 pp.

Steinitz, W. 1929. Die Wanderung Indopazifischer Artens ins Mittelmeer seit Beginn der Quarter-periode. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie, Leipzig* **22:** 1-90.

Stewart, R. B. 1930. Gabb's California Cretaceous and Tertiary type lamellibranchs. *Publications of the Academy of Natural Sciences, Philadelphia* **3:** 1-314.

Sturany, R. W. A. 1901. Expedition S.M. Schiff 'Pola' in das Rothe Meer, nördliche und südliche Hälfte 1895/96 und 1987/98. XIV. Zoologische Ergebnisse. Lamellibranchiaten des Rothen Meeres. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaften Classe* **68:** 255-295.

Sturany, R. W. A. 1905. Beiträge zur Kenntnis der Molluskenfauna des Rothen Meeres und des Golfes von Aden. *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft* **37:** 132-146.

Swainson, W. 1840. *A treatise on malacology, or shells and shellfish.* (Longman *et al.*, London), viii + 419 pp.

Taylor, J. D. & Reid, D. G. 1984. The abundance and trophic classification of molluscs upon coral reefs in the Sudanese Red Sea. *Journal of Natural History* **18:** 175-209.

Tenison Woods, J. E. 1878. Census; with brief descriptions of the marine shells of Tasmania and the adjacent islands. *Papers and Proceedings of the Royal Society of (Van Diemen's Land) Tasmania* **(1878):** 3-34.

Teppner, W. von 1922. Lamellibranchiata tertiaria, Pars 15. "*Anisomyaria*" II, *in*: 'Fossilium Catalogus I: Animalia'. Diener, C. (ed.), (Junk, Berlin), pp. 67-296.

Thayer, C. W. 1975. Function of the oblique resilium in *Juxtamusium* (Bivalvia, Pectinidae): A balanced adaptive system. *Proceedings of the Malacological Society of London* **41:** 447-449.

Thompson, E. F. 1939. Chemical and physical investigations. The exchange of water between the Red Sea and Gulf of Aden over the 'sill'. *Scientific Reports. The John Murray Expedition 1933-34.* Vol. **2(4):** 105-119.

Thornley, G. 1968. Checklist of the pectens of Australia, with critical comments. Part 2. *Australian Newsletter* **15(60):** 9-13.

Thorson, G. 1971. Animal migrations through the Suez Canal in the past, recent years and the future (a preliminary report). *Vie et Milieu* **2:** 841-846.

Tillier, L. & Bavay, A. 1905. Les mollusques testacés du canal de Suez. *Bulletin de la Société Zoologique de France* **32(12):** 170-181.

Tomlin, J. R. le B. 1927. Cambridge Expedition to the Suez Canal, 1924. XVIII. Report on the Mollusca (Amphineura, Gastropoda, Scaphopoda, Pelecypoda). *Transactions of the Zoological Society of London* **22:** 291-320.

Tomlin, J. R. le B. & Salisbury, A. E. 1928. Laborde's 'voyage' and the Mollusca therein described by Deshayes. *Proceedings of the Malacological Society of London* **18:** 32-35.

Trew, A. 1987. *James Cosmo Melvill's new molluscan names.* (National Museum of Wales, Cardiff), 84 pp.

Tryon, G. W. 1869-70. Description of new species of marine bivalve Mollusca in the collection of the Academy of Natural Sciences. *American Journal of Conchology* **5:** 170-172.

Vaillant, L. 1865. Recherches sur la faune malacologique de la baie de Suez. *Journal of Conchology* **13:** 97-121.

Vaught, K. C. 1989 [Abbott, R. T. & Boss, K. J., eds]. *A classification of the living Mollusca.* (American Malacologists Inc., Melbourne, U.S.A.), xii + 195 pp.

Viader, R. 1937. Revised catalogue of the testaceous Mollusca of Mauritius and its dependencies. *Bulletin of the Mauritius Institute* **1(2):** i-xiii, 1-111.

Wagner, H. P. 1984. *Chlamys (Chlamys) liltvedi* n. sp. (Pectinidae), a newspecies from South Africa. *Basteria* **48:** 3-6.

Waller, T. R. 1972. The Pectinidae (Mollusca: Bivalvia) of Eniwetok Atoll, Marshall Islands. *Veliger* **14(3):** 221-264.

Waller, T. R. 1978. Morphology, morphoclines and a new classification of the Pteriomorphia (Mollusca: Bivalvia). *Philosophical Transactions of the Royal Society of London,* **B, 284:** 345-365.

Waller, T. R. 1984. The ctenolium of scallop shells: functional morphology and evolution of a key family-level character in the Pectinacea (Mollusca: Bivalvia). *Malacologia* **25(1):** 203-219.

Waller, T. R. 1986. A new genus and species of scallop (Bivalvia: Pectinidae) from off Somalia, and the definition of a new tribe Decatopectinini. *Nautilus* **100(2):** 39-46.

Waller, T. R. 1991. Evolutionary relationship among commercial scallops (Mollusca: Bivalvia: Pectinidae), in:'Scallops: biology, ecology and aquaculture'. Shumway, S. E. (ed.), (Elsevier, Amsterdam, etc.), pp. 1-73.

Waller, T. R. 1993. The evolution of "*Chlamys*" (Mollusca: Bivalvia: Pectinidae) in the tropical western Atlantic and eastern Pacific. *American Malacological Bulletin* **10:** 195-249.

Waller, T. R. & Marincovich Jr., L. 1992. New species of *Camptochlamys* and *Chlamys* (Mollusca: Bivalvia: Pectinidae) from near the Cretaceous/Tertiary Boundary at Ocean Point, North Slope, Alaska. *Journal of Paleontology* **66(2):** 215-227.

Wang, Z. 1983a. Studies on Chinese species of the family Pectinidae, 2. Chlamydinae (A new species and three new records of the genus *Cryptopecten*). *Oceanologia et Limnologia Sinica* **14(4):** 402-406 [In Chinese].

Wang, Z. 1983b. Studies on Chinese species of the family Pectinidae, 3. Chlamydinae (1. *Chlamys*). *Transactions of the Chinese Society of Malacology* **1:** 47-56 [In Chinese].

Wang, Z. 1983c. Studies on Chinese species of the family Pectinidae, 3. Chlamydinae (genus *Bractechlamys*). *Oceanologia et Limnologia Sinica***14(6):** 531-535 [In Chinese].

Wang, Z. 1985. Studies on Chinese species of the family Pectinidae, 7. Chlamydinae (Genus *Semipallium*). *Oceanologia et Limnologia Sinica* **16(6):** 502-505 [In Chinese].

Whiteaves, J. F. 1893. Notes on some marine Invertebrata from the coast of British Columbia. *Ottawa Naturalist* **7:** 133-137.

Wilkes, J. 1810. Conchology, *in:* 'Encyclopaedia Londinensis; or, Universal Dictionary of Arts, Sciences, and Literature'. (Adlard, London), pp. 14-41.

Winckworth, R. 1932. The British marine Mollusca. *Journal of Conchology* **19(7):** 211-252.

Wood, W. 1825. *Index testaceologicus; or a catalogue of shells, British and foreign* [...]. (W. Wood, London), xxxii + 188pp.

Woolacott, L. [1955]. Coral dwellers. *Proceedings of the Royal Zoological Society of New South Wales* **(1953-54):** 79-81.

Yaron, I., Schiøtte, T. & Wium-Andersen, G. 1986. A review of molluscan taxa described by P. Forsskål & C. Niebuhr with citation of original descriptions, discussion of type-material avaiable and selection of some lectotypes. *Steenstrupia* **12(10):** 157-203.

Yokoyama, M. 1924. Mollusca from the coral-bed of Awa. *Journal of the College of Science, Imperial University of Tokyo* **45(1):** 56-57.

Yonge, C. M. 1967. Observations on *Pedum spondyloideum* (Chemnitz) Gmelin, a scallop associated with reef-building corals. *Proceedings of the Malacological Society of London* **37:** 311-323.

Table I: Number of samples of each of the 22 taxa.

Species	MO	HD	HUJ	ISRSE	NS	ZMUC	Total
Propeamussiidae							
Parvamussium formosum	35	-	6	1	-	-	42
Parvamussium siebenrocki	14	-	2	-	-	-	16
Parvamussium thyrideum	3	-	-	-	-	-	3
Similipecten eous	21	-	3	-	-	-	24
Pectinidae							
Delectopecten musorstomi	3	-	-	-	-	-	3
Decatopecten amiculum	-	3	1	-	-	-	4
Decatopecten plica	-	3	3	5	2	-	13
Excellichlamys spectabilis	1	3	4	-	-	-	8
Glorichlamys quadrilirata	-	1	-	-	-	-	1
Gloripallium maculosum	-	6	4	-	2	1	13
Gloripallium pallium	-	5	-	-	-	-	5
Juxtamusium maldivense	20	5	3	-	2	-	30
Mirapecten yaroni n. sp.	1	7	3	-	1	1	13
Pecten erythraeensis	3	-	1	-	1	-	5
Coralichlamys madreporarum	-	2	-	-	-	-	2
Laevichlamys rubromaculata	-	12	7	-	5	1	25
Laevichlamys superficialis	3	9	11	-	2	1	26
Pedum spondyloideum	-	2	4	-	-	-	6
Semipallium crouchi	2	7	4	-	-	-	13
Mimachlamys andamanica	10	6	1	-	-	-	17
Mimachlamys senatoria	1	10	6	14	1	-	32
Cryptopecten nux	33	-	7	-	3	-	43
Total	**150**	**81**	**70**	**20**	**19**	**4**	**344**

Table II: Vertical range (meters).

Species	All samples	"Live" specimens and united valves () number of samples
Propeamussiidae		
Parvamussium formosum	30-35 to 700-740	-
Parvamussium siebenrocki	121 to 700	-
Parvamussium thyrideum	137-146 to 320	-
Similipecten eous	80 to 690	-
Pectinidae		
Delectopecten musorstomi	121 to 350	-
Decatopecten amiculum	4 to 20-30	4 to 20-30 (2)
Decatopecten plica	0-4 to 20-40	9-12 to 20-24 (2)
Excellichlamys spectabilis	4-8 to 10-15	4-8 to 10-15 (3)
Glorichlamys quadrilirata	20-25	20-25 (1)
Gloripallium maculosum	0 to 20	beach (3)
Gloripallium pallium	2-4 to 20-25	2-4 to 20-25 (5)
Juxtamusium maldivense	6-8 to 60-90	6-8 to 73-82 (6)
Mirapecten yaroni n. sp.	2-5 to 121	4-15 to 68 (8)
Pecten erythraeensis	15-20 to 37-49	42-46 (1)
Coralichlamys madreporarum	4-8 to 18	4-8 to 18 (2)
Laevichlamys rubromaculata	2-4 to 24-28	2-4 to 24-28 (11)
Laevichlamys superficialis	0.5-2 to 15	0.5-2 to 15 (9)
Pedum spondyloideum	10-18 to 26	10-18 to 26 (2)
Semipallium crouchi	10-12 to 132-137	10-12 to 25-30 (8)
Mimachlamys andamanica	1.5 to 170-270	1.5 to 15-20 (5)
Mimachlamys senatoria	0 to 55	9-12 to 55 (15)
Cryptopecten nux	40-49 to 410	40-50 to 64-73 (4)

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Freshwater snails of the genus *Gyraulus* (Planorbidae) in Australia: the taxa of Tasmania

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Abstract

The classification of freshwater snails belonging to the genus *Gyraulus* (Basommatophora: Planorbidae) from Tasmania is revised according to morphological observations on type materials, other shells collected in the 19thC, and about 920 alcohol-preserved specimens from 17 localities and mostly collected during the last 30 years. Four species-group taxa (*atkinsoni, meridionalis, scottianus, tasmanicus*) have previously been named from shells collected in Tasmania; two of these are type species for genera named by Iredale (1943) (*meridionalis* for *Plananisus, scottianus* for *Pygmanisus*). The present observations on the shell and body (pigmentation, kidney, intestinal loop and genital organs) suggest that there are two widely distributed species, *G. meridionalis* (including *tasmanicus* as a synonym) and *G. scottianus*. Lectotype material for *G. meridionalis* is designated here, from Circular Head, Tasmania. Although *G. atkinsoni* may be a conspecific form of *meridionalis*, it is maintained here as a distinct species in order to encourage further study of this depressed and sharply keeled form of shell. Descriptions are given of *G. mienanus* sp. n. from Great Lake and *Gyraulus* sp., another lacustrine form and possibly a distinct species, found in Lake Sorell. These two lacustrine taxa, and also *G. meridionalis* and *G. atkinsoni* are placed in *Gyraulus sensu stricto*, though with some doubt as in this group of Tasmanian taxa the position of attachment of the penis within the penis sheath differs from that previously known in this subgenus. If this difference should prove sufficient to define a new subgenus, its name could be *Plananisus* Iredale, 1943. Differences between *G. scottianus* and other Australian species, in the shell, kidney and penial structure, are sufficient to rank *Pygmanisus* Iredale as a subgenus. However, this taxon appears closely similar to *G. (Torquis)* of N America, Europe and western central Asia, suggesting the possibility that it has been introduced into Australia since European settlement. Further investigations are needed to determine the relationships between the *Gyraulus* faunas of Tasmania and mainland Australia To achieve fuller understanding of *Gyraulus* in Australia, morphological data need to be supplemented by molecular genetics and ecological studies.

Key words: Planorbidae, *Gyraulus*, freshwater snail, taxonomy, Australia, Tasmania

Introduction

Gyraulus (Planorbidae) is a genus of small freshwater snails, usually discoid and planispiral (in some ancient lakes pseudodextral with a spire). The whorls vary in shape between species, (and sometimes within them), from rounded to acutely angular and may be keeled (carinate). The penis has a sub-terminal opening and the tip bears a chitinised stylet, either dagger-like or of hobnail form. The genus occurs worldwide except for South America south of Venezuela. Among the more recent taxonomic investigations, the most comprehensive focussed upon the taxa inhabiting Europe and Asia (Meier-Brook, 1983), and studies have been carried out for smaller areas of southern Africa (Brown & Van Eeden, 1969) and south-eastern Australia (Brown, 1981).

The penial morphology distinguishes *Gyraulus* from certain other planorbid genera that despite their similar shell forms have very different chitinised penial armature and are found in Africa. One impetus to the study of Australian planorbids with this form of shell is to discover whether any group apparently endemic to Africa is present also in Australia. Twenty-five species-

group taxa named from Australian materials and which are candidates for inclusion in *Gyraulus* were listed by Iredale (1943; under *Pygmanisus, Plananisus* and *Glyptanisus*). All these taxa were known only from shells. Apparently the first anatomical observations were not made until the 1970s (Brown, 1981; Meier-Brook, 1983, 97-98); all copulatory organs examined were found to have the penial structure characteristic of *Gyraulus*. Smith & Kershaw (1979, 1981) following discussion with Meier-Brook, reported the presence of 3 species of *Gyraulus* in SE Australia including Tasmania (Table 1). In a faunal catalogue, Smith (1992) maintained *Pygmanisus* as a genus distinct from *Gyraulus*; the taxonomic position of additional species-group taxa, including two originating from Tasmania (Table 1), was regarded as uncertain and they were listed as incertae sedis.

The number of valid species of *Gyraulus* living in Australia is likely to be far fewer than the total of named species-group taxa. Their original descriptions are mostly brief and often refer to shell characters that seem trivial. Four of these taxa have type localities in Tasmania; all were described in the 1870s and they are pre-dated only by one taxon named from the Australian mainland, *Planorbis gilberti* Dunker, 1848 of "New Holland". The Tasmanian taxa include the type species for Iredale's genera *Plananisus* and *Pygmanisus*. No anatomical data has been previously published for any snails from Tasmania with a *Gyraulus*-like shell. To improve knowledge of the Tasmanian representatives of this genus is fundamental to achieving a more satisfactory classification for these snails in mainland Australia.

The first aim of this study was to establish more clearly the characterisations of taxa referable to *Gyraulus* and previously named from shells collected in Tasmania, by means of type material and the literature. Supplementary information about shell variation and soft part morphology was obtained, so far as possible, from materials collected within recent decades. In the course of elucidating concepts of species held by 19thC authors it emerged that shells from Great Lake, in the highlands of Tasmania, belong to a species new to science that is described herein. The status of the different taxa was assessed in the light of the morphological findings, and a revised classification is suggested (Table 1). The need is evident to supplement morphological data by the more direct evidence of genetic affinities obtainable by allozyme electrophoresis and molecular sequencing. I hope that the application of such techniques will be encouraged by this attempt to clear pathways into what might appear to be an impenetrable thicket of classical taxonomy.

Materials

Details of materials are given under species-group taxa; localities are shown in Fig. 1. "Wet" = preserved in ethyl alcohol. Museum acronyms are:

AMS - Australian Museum, Sydney;
BMNH - Natural History Museum, London;
QVM - Queen Victoria Museum, Launceston;
SAMA - South Australian Museum, Adelaide;
TMH - Tasmanian Museum and Art Gallery, Hobart;
ZMB - Zoological Museum of the Humboldt University, Berlin.

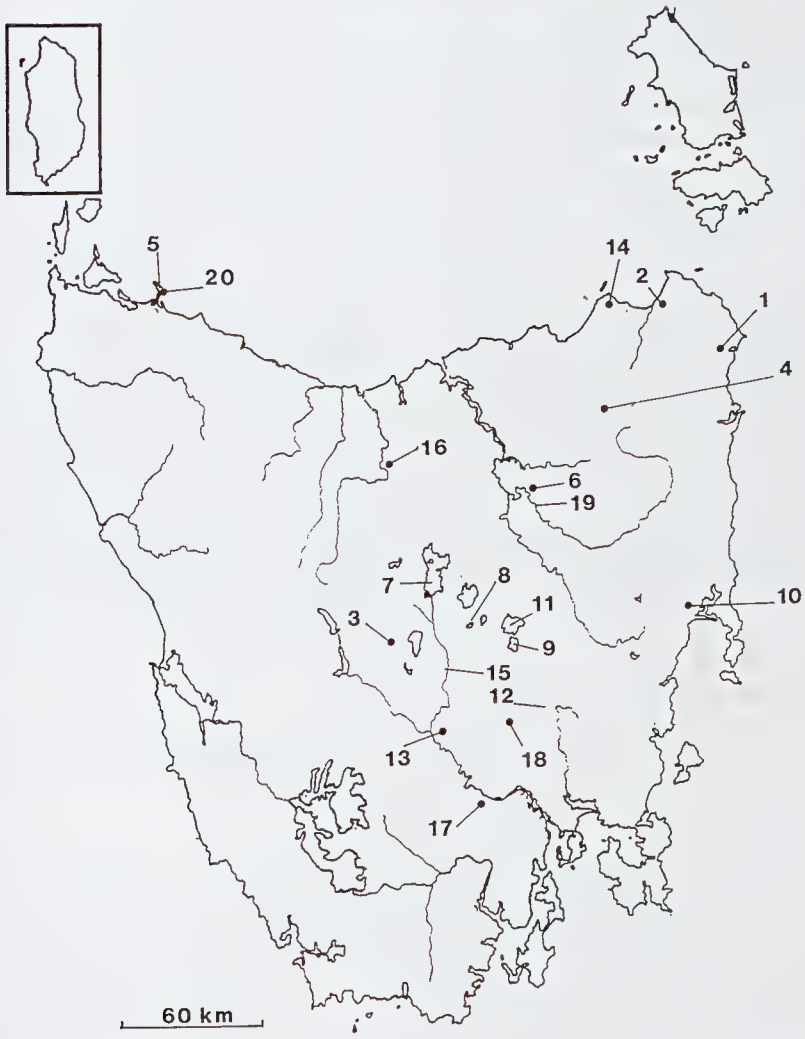

Figure 1.
Tasmania, showing distribution of collecting sites for materials of *Gyraulus* reported on in this paper. **1,** Ansons River. **2,** Bowlers Lagoon. **3,** Brown Marsh Creek, Lyell Highway. **4,** Carries Brook, south of Ringarooma. **5,** Circular Head. **6,** Evandale. **7,** Great Lake. **8,** Lagoon of Islands. **9,** Lake Crescent. **10,** Lake Leake. **11,** Lake Sorell. **12,** Lake Tiberias. **13,** Lawrenny, Ouse. **14,** Marys Puddle, near Waterhouse Point. **15,** Ouse River. **16,** Pipers Lagoon Creek, Bridgenorth Road. **17,** Redlands Lagoon, Plenty River. **18,** River Jordan, near Apsley. **19,** South Esk River. **20,** Stanley.

Methods

Shell

Preparation: Many of the shells examined were coated to some extent with a reddish brown deposit, which was removed in a saturated aqueous solution of oxalic acid, in order to count the whorls accurately and to examine the microsculpture.

Descriptive terms and orientation: Descriptive terms are used in the same sense as Meier-Brook (1983), apart from those related to the orientation of the shell. The profile (peripheral) view of the shell is here illustrated as pseudodextral, i.e. with its aperture on the reader's righthand side (Fig. 2B), as in previous publications on *Gyraulus* in Australia (apart from Cotton, 1943, who placed these views vertically on the page). This is a matter of convention and convenience, to myself at least, for the purpose of comparison; it has the further advantage that the underside of the figured shell corresponds to the functional underside in life, the shell being carried generally sloping towards the animal's left side. However, since *Gyraulus* is anatomically sinistral, some authors, including Meier-Brook (1983), present profile views with the aperture at the left as viewed by the observer. An unfortunate effect of the difference in orientation is that the side referred to as the underside in the first position is the upperside in the second position, and vice versa (see remarks in Meier-Brook, 1983, pp. 5 and 27). In order to avoid the confusion inherent in applying the words underside and upperside to such a shell, I follow Malek (1985) in using the terms left side (= underside of Brown, 1981 and upperside of Meier-Brook, 1983) (Fig. 2A) and right side (= upperside of Brown, 1981 and underside of Meier-Brook, 1983). Further information about the shell is given in the review of characters below.

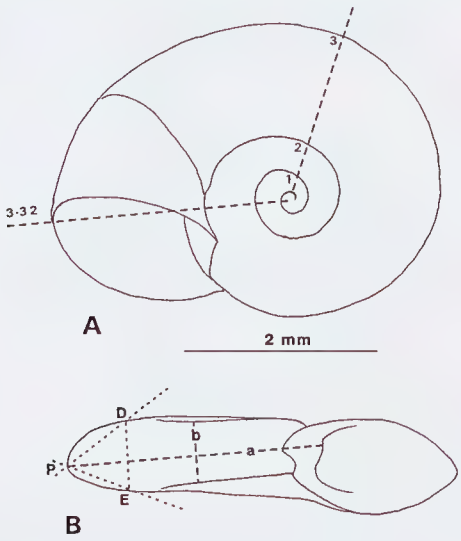

Figure. 2.
A, Left side of *Gyraulus meridionalis,* showing method of measuring the number of whorls. First the completed whorls were counted along an axis fitted by eye to the proximal curve of the protoconch in a drawing of the shell. A protractor placed on the drawing was then used to determine the extent of any uncompleted whorl, measuring to the outermost point on the apertural lip. **B,** Profile view of shell, showing the depression angle (DEP) and dimensions (a) and (b), which were used to calculate the flatness index (a/b). (a) was measured along a line constructed to span the greatest diameter of the last whorl less the aperture; (b) is the height of the whorl perpendicular to the mid-point of (a). The depression angle (DEP) is subtended by the two lines that pass from the outermost point on the periphery (E) to points D and P, located by constructing a line perpendicular to (a) at one quarter of its length from E.

Measurements: All measurements were taken from drawings of shells at magnification x25 made by means of the Wild M5 microscope with drawing attachment. The method for measuring the number of whorls (Fig. 2A) followed those of Mandahl-Barth (1958, fig. 1) and Meier-Brook (1983, fig. 1). First a line was drawn on the outline of the left side of the shell, fitted by eye to the proximal curve of the protoconch. The number of whorls to the outermost point of the apertural lip was measured to the nearest 0.01 of a whorl by means of a protractor placed on the drawing. Depression of the shell was measured as the proportional relationship between dimensions "a" and "b" (Fig. 2B), the flatness index (a/b) (Brown & Van Eeden,1969; Meier-Brook, 1983).

Variation in the shape of the periphery of the *Gyraulus* shell is easily observed and the degree of angulation is mentioned in most taxonomic descriptions. Yet no quantitative measure of angulation has been proposed and I have failed to devise one that is satisfactory. The method used by Goodfriend (1983) to measure the so-called peripheral angle in the landsnail *Pleurodonte* is at first sight attractive, but what it measures essentially is the depression of the whorl rather than angularity in the shape of the whorl. There is no necessary correlation between an acute angle measured by this technique and the presence of an angular or keeled (carinate) periphery. Using Goodfriend's method the peripheral angle obtained for a depressed shell with a rounded periphery may be the same as the angle measured for a shell with an acutely angular periphery. Though not a reliable index of angularity, Goodfriend's "peripheral angle" was measured in this study, in order to compare its discriminatory value with the flatness index a/b. To make the meaning of this angle clearer it is here re-named the depression angle (Fig. 2B, DEP).

Anatomy

Preserved animals were dissected, which were contracted to a varying degree, with the head/foot projecting a little from the aperture or retracted up to one-third of a whorl. Reproductive organs and the kidney were stained in safranin and mounted in Canada balsam. Radulae were examined under the optical microscope after staining in Mallory's stain (Brown, 1980: 442) and mounting in Canada balsam. Rudimentary teeth lacking distinct cusps were disregarded when counting the number of transverse rows and the number of teeth in a row.

Review of morphological features and characters included in the systematic descriptions

Shell

Maximum diameter: measured from the outermost part of the lip to the opposite periphery.

Number of whorls: total, including the protoconch.

Depression: measured by the flatness index (ratio a/b) and the depression angle (DEP).

Shape of periphery: evenly rounded, subangled or angled and with or without a keel (carina).

Fringe: peripheral angle or keel with or without a fringe of periostracum. May be difficult to determine for dry shells, on which the periostracum may be

damaged or entirely missing. Although described as a "periostracal collar" by Meier-Brook (1983, p. 26), the fringe is not actually a continuous band but a composite structure of numerous overlapping lamellae of periostracum, crossing the periphery obliquely and attached to the larger of the transverse ridges in the underlying shell.
Shape of shells on the left and right sides: concave to varying degrees. Shape of whorls, above and below the periphery: varying from shallowly to steeply curved to subangular and angular.
Aperture deflection: attachment of lip deflected to an extent that depends on inclination of the last whorl away from the horizontal and towards the left side.
Microsculpture of teleoconch: including transverse growth lines (ridges and hollows), spiral ridges and spiral striae. Commonly the numerous fine transverse ridges are interrupted by spiral striae, forming spiral tracks of short ridges, here termed 'riblets'.

Radula
All the radulae examined were of the same general form found in other studies of *Gyraulus* (e.g. Meier-Brook, 1983; Jung & Burch, 1990); basically with a bicuspid central and tri-cuspid lateral/marginal teeth (not clearly divisible into two classes of tooth, see Burch & Jeong, 1984). Few denticles were seen in the present material and these were much smaller than those described by Burch & Jeong (1984) for *G. essingtonensis*. Yet it is difficult to define taxonomic characters at the species level in *Gyraulus* (see Meier-Brook, 1983: 12) and details are not included in the present descriptions.

Head-foot
Pigmentation lacking or diffusely grey.

Mantle roof pigmentation
Border with or without band (grey to black), roof of pallial cavity with diffused pigment or a distinct pattern. An orange-brown patch may be present mid-anteriorly, between the ureter and the mantle border.

Kidney
Margins straight or undulate and folded inwards, forming partial partitions termed 'septa' by Meier-Brook (1983). Yung & Burch (1990) commented that strictly speaking the kidney is not septate, since it is not divided into separate compartments, the lumen following continuously the sigmoid bends of the kidney walls. The term 'septate' is used here in the sense of Meier-Brook (1983). In the present study a few well-defined septa were observed in one kidney of *G. meridionalis*, which was usually non-septate.

Intestine
Either straight or with posterior loop of varying length.

Reproductive system
Ovotestis: number of lobes (acini). Difficult to determine precisely because the

lobes are poorly differentiated at the proximal end of the ovotestis.
Seminal vesicle: with varying number of convolutions, which may be bulbous or spinous (Meier-Brook, 1983, fig. 20).
Copulatory organ: total length and relative proportions of preputium and penis sheath.
Penis: position of attachment within penis sheath, distance of penial pore from the tip, shape of tip, shape of the penial stylet.
Prostate gland: variable number of lobes.
Bursa copulatrix: of various shapes classified by Meier-Brook (1983, fig. 33G).

Systematics

Gyraulus (Charpentier, 1837)

Shell planispiral or rarely (in some ancient lakes) pseudodextral with an elevated spire. From 2 to 10mm in diameter, with 3 to 5 whorls, which may be rounded, angular or keeled. Penis with a sub-terminal opening and a chitinous stylet, which is commonly dagger-like. Other planispiral genera with this type of penial stylet differ from *Gyraulus* in the proportional height of the whorls and the slower rate of whorl increase (e.g. Meier-Brook, 1983, figs 109, 110).

Subgenus **Gyraulus** sensu stricto

Shell planispiral, though last whorl may be somewhat descending; kidney margins straight; prostate diverticula between 8 and 40 in number (see further, Meier-Brook, 1983, 99-100).

Gyraulus meridionalis (Brazier, 1875)
(Figs 2-15, 18)

Planorbis meridionalis Brazier, 1875: 20; - Tenison-Woods, 1879: 69; - Johnston, 1891: 145; - Tate & Brazier, 1882: 559; - Petterd, 1889: 63 (in part, non pl. 1, figs 4-6); - May, 1921a: 70, pl. 10, fig. 11; 1921b: 90, 1923: pl. 41, fig. 17; - Gabriel, 1939: 122 (in part).
Planorbis brazieri Clessin, 1885: 166 (in part; the specimens from Tasmania, Mus. Berol. Nr. 18900).
Glyptanisus meridionalis - Iredale, 1943: 225 (in part); - Cotton, 1943: 148 (probably not pl. 18, figs 15 and 16).
Glyptaniscus [sic] *meridionalis* - May & Macpherson, 1958: pl. 41, fig. 17.
Gyraulus meridionalis - Smith & Kershaw, 1979: 89, text-fig.; 1881: 61, text-fig.; - Smith, 1992: 270.

Original description: "Shell discoid, light horny brown, faintly marked with oblique lines of growth, sharply carinated at the periphery, whorls 3, the last large, more than half the size of the whole shell; large in front, moderately convex, spire depressed, base convex, depressed in the centre of the whorls, aperture oblique, hatchet shaped, peristome thin, acute, margins approximating the right joined to the left by a thin deposit of calius[sic]. Diam. maj. $1^{3}/4$, min. $1^{1}/4$, alt. $^{1}/2$ line [equivalent to measurements in mm of 3.71, 2.65 and 1.06]. Hab. Ouse River, Tasmania, Mr. Masters. Circular Head, [ditto] Petterd."

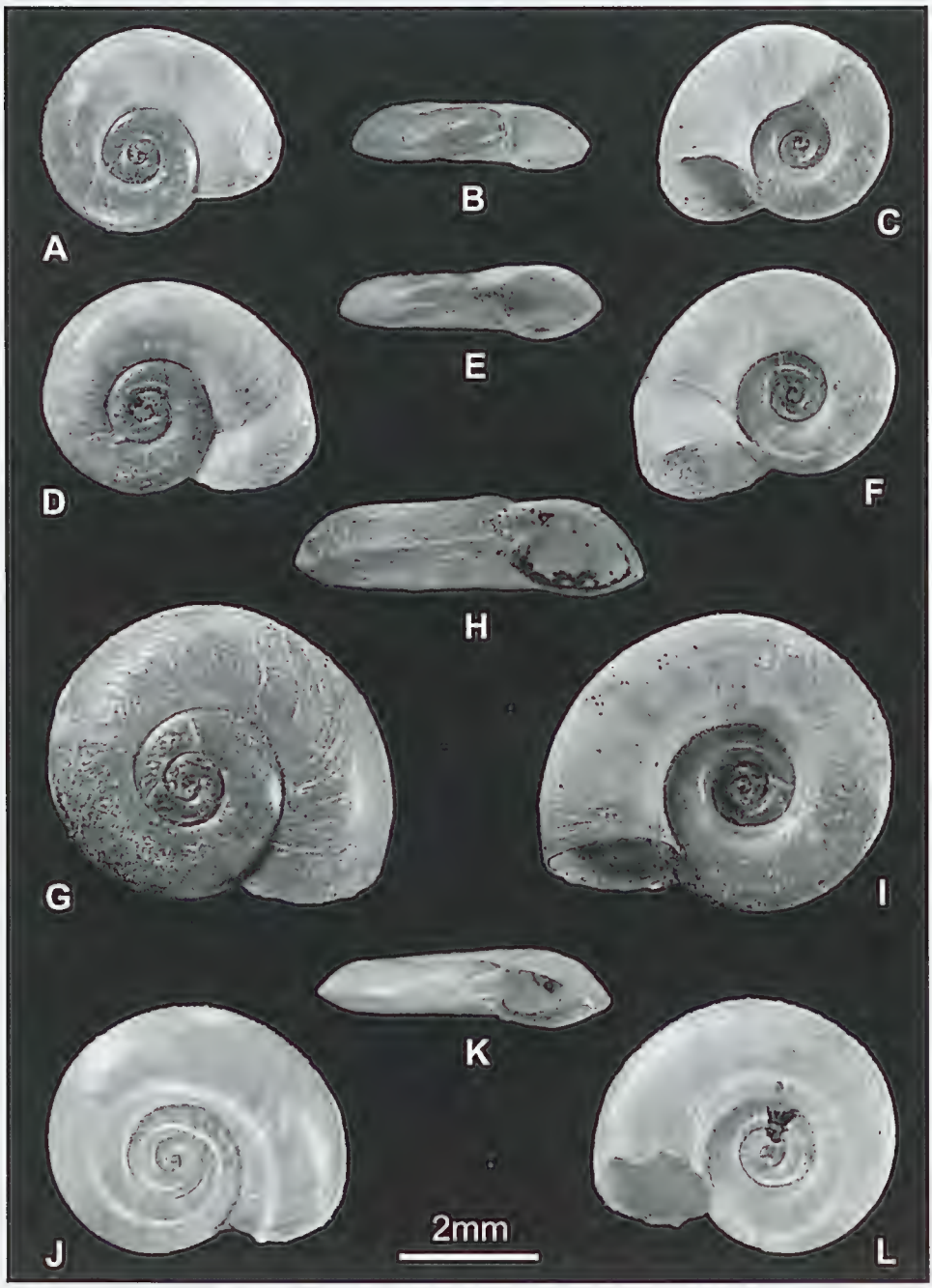

Figure 3.
Shells of *Gyraulus meridionalis*. **A,B,C;** lectotype (AMS 100598; Circular Head). **D,E,F;** paralectotype from Circular Head. **G,H,I;** paralectotype from Ouse River (QVM:9:116). **J,K,L;** from near Stanley (AMS C314279).

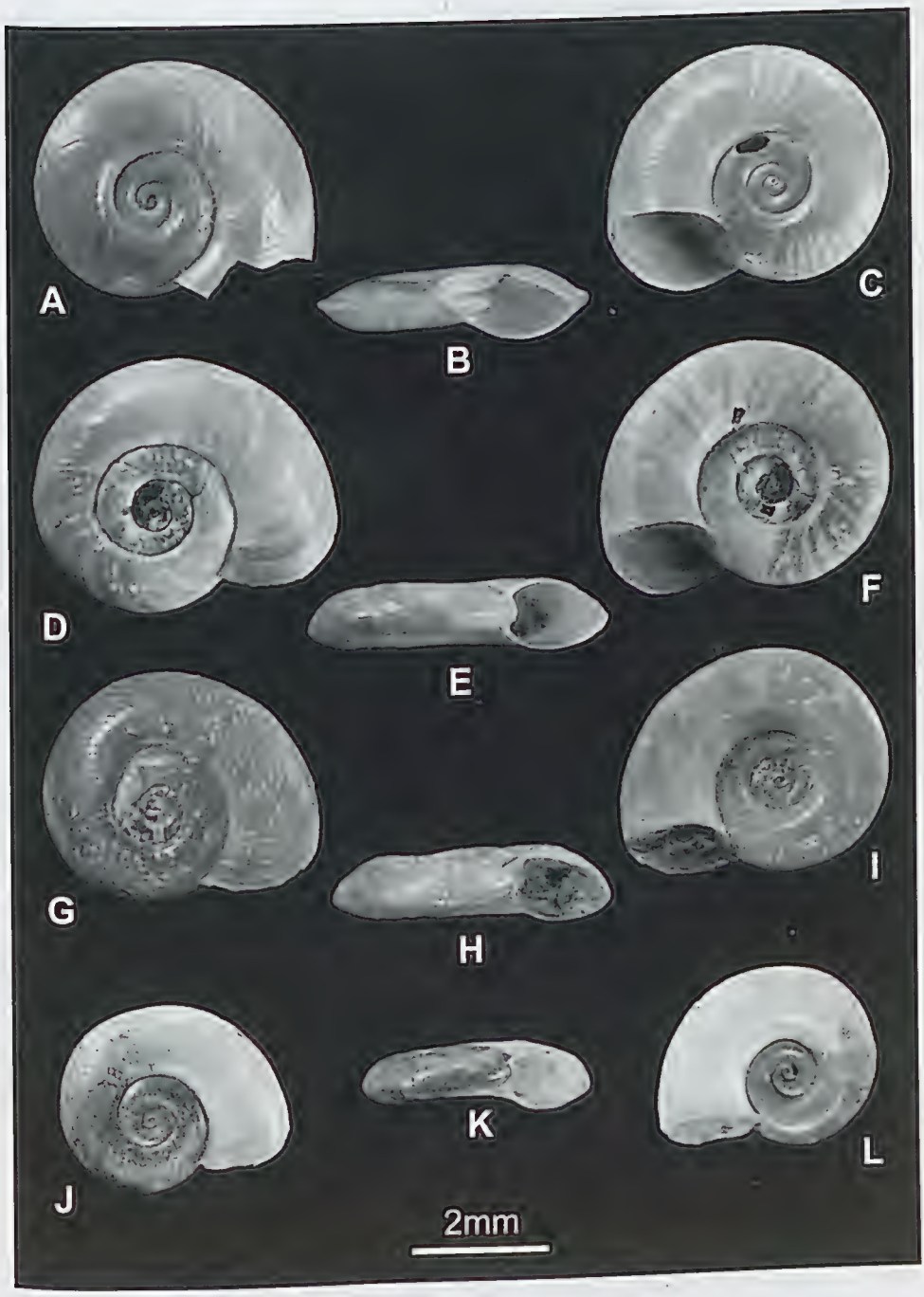

Figure 4.
Shells of *Gyraulus*. **A-I,** *G. meridionalis*. **A-F;** from Lagoon of Islands (TMH E12333). **G,H,I;** From Tasmania and identified by Clessin as *G. brazieri* (ZMB 18900). **J,K,L;** *G. tasmanicus,* possible syntype (TMH E872).

Type locality (following designation of lectotype): Tasmania, Circular Head [the peninsula containing the town of Stanley, on the north-west coast of Tasmania].

Additional materials examined:
ZMB Moll. 18900 (5 dry). Tasmania, leg. Krafft [reported by Clessin, 1885 under *Planorbis brazieri*]. AMS C314271 (40 wet). Lake Tiberias (Tasmania), near lake house on southern edge; 42°26.5′S, 147°21.783′E, alt. 460m; on roots, stems, leaves of water plants; 3 Feb. 1987, W.F. Ponder, J.H.Waterhouse and G.A. Clark. AMS C314273 (140 wet). Pipers Lagoon Creek, Meander River at Bridgenorth Road, west of Launceston; 41°26.5′S, 146°26.5′E; alt. 220m; 26 Jan. 1987, stn TA53, W.F. Ponder, J.H. Waterhouse and G.A. Clark. AMS C314274 (2 wet). Ansons River, The Bottleneck, on Ansons Bay Road, from rock and weed; 41°3.7′S, 148°138′E; alt. 10m; stn TA96, W.F. Ponder, J.H. Waterhouse and G.A. Clark. AMS C314277 (10 wet). South Esk River, in gorge between First and Second Basin, Launceston; 41°25.967′S, 147°7.95′E; alt. 10m; on and under rocks; 8 Feb. 1987, stn TA142, W.F. Ponder and G.A. Clark. AMS C314278 (95 wet). Lake Crescent, at drain on west side; 42°10.2′S, 147°8.9′E; alt. 800m; 3 Feb. 1987, W.F. Ponder, J.H. Waterhouse and G.A. Clark. AMS C314279 (22 wet). Drainage ditch, 0.5 mile from Stanley, on main road; 40°46′S, 145°18′E; 2 Jan. 1975. Presented by G.A.D. Davis. QVM:9:7854 (17 dry). South Esk River, ex Petterd collection [two groups of specimens, see under Shell]. QVM:9:11334 (9 wet). NE Tasmania, Marys Puddle, near Waterhouse Point, EQ535784, 9 Oct. 1991, TJL and LFM. TMH E9986 (1 wet). Arthur Lake, morass, 11 Jan. 1960, B.C. Mollison. TMH E12333 (120 wet). Lagoon of Islands, in fine submerged weed near shore, 30 Jan. 1965, B.C. Mollison. TMH E16458 (12 dry). Lagoon of Islands, 20 Feb. 1964, B.B. Mollison. TMH E2406 (6 wet). Lake Leake, Nov. 1937, J.W. Evans.

Type materials examined: Lectotype (here designated), AMS C100598 Tasmania, Circular Head, ex Brazier collection. Paralectotypes: AMS C100598 (38 dry); QVM:9:116 (2 dry) Tasmania, Ouse River, ex Petterd collection.

Shell (Figs 2-7, Table 2): The lectotype and paralectotypes from Circular Head (Fig. 3A-F) have the whorls moderately depressed, with a peripheral angle of varying strength, situated a little towards the left side. They reach about 4mm in diameter and nearly 3.4 whorls (Fig. 5). Flatness index a/b 3.57 to 4.40 (Fig. 6), increasing with (a) due to the tendency of the shell to become more depressed with increasing size. This growth pattern results in the depression angle decreasing with shell size (Fig. 7). Periphery subangled to distinctly angled, generally more acutely so in the larger shells, with a whitish blunt keel on some parts of some shells; no fringe was seen (though it would not be necessarily evident in dry shells). Whorls 1-3 on the right side are only slightly sunken; left side much more concave, the last whorl increasing rapidly in the larger shells and embracing the inner whorls deeply. Much of the left surface of the last whorl is only weakly curved or is nearly flat, especially so approaching the lip. The attachment of the lip of large shells is mostly to the left half of preceding whorl, due to deflection of the last whorl. Microsculpture strongest on the left side, where the numerous fine transverse ridges are divided into short riblets by spiral striae.

Dimensions of shells from selected from the lectotype series from Circular Head:

	whorls	diameter	a	b	a/b
Lectotype	3.30	3.49	2.51	0.62	4.15
Paralectotypes					
smallest	2.74	2.76	1.89	0.51	3.70
largest	3.37	4.07	2.66	0.62	4.40

Two paralectotypes from the Ouse River (QVM:9:116) (Fig. 3G,H,I) have values for a/b similar to shells in the lectotype series from Circular Head, but at a considerably larger size (Fig. 6). Shells of this size (over 5mm diameter) would be expected to be more depressed (giving higher values for a/b) if they had grown according to the same ontogenetic pattern, yet all the paralectotypes seemed conspecific on consideration of the whole assemblage of shell characters. If the shells from Circular Head are not fully grown, an indication of their final form is perhaps to be seen in specimens recently collected from near Stanley (see below).

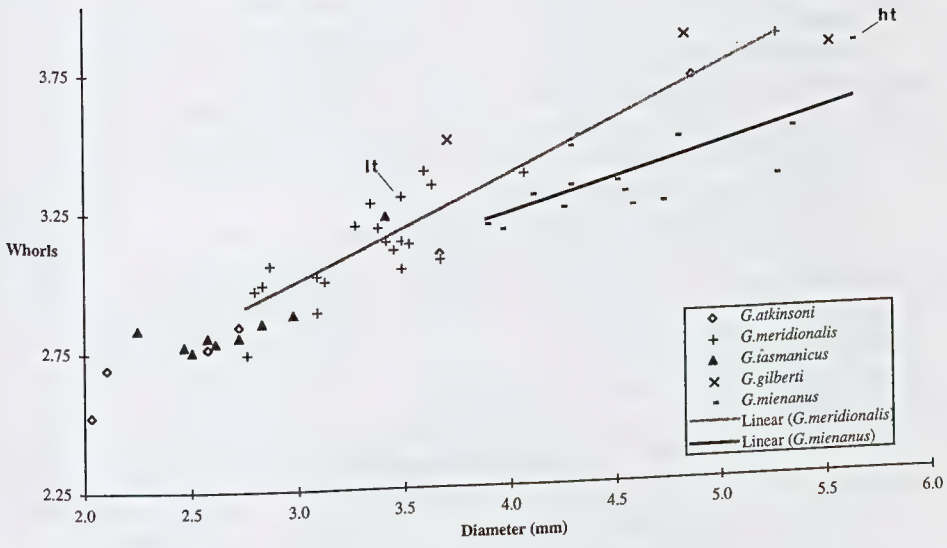

Figure 5.
Number of whorls plotted against diameter for shells of *Gyraulus*. *G. atkinsoni:* 6 possible syntypes, TMH E879. *G. meridionalis:* lectotype (lt), 19 paralectotypes from Circular Head (AMS 100598) selected to represent the size range and 1 paralectotype from Ouse River (QVM:9:116) isolated at the righthand side of the distribution. *G. tasmanicus:* 9 specimens being probable type material, TMH E872. *G. gilberti:* 3 syntypes (BMNH 1969146). *G. mienanus* sp.n.: holotype (ht), 5 paratypes (QVM:9:7857, 7862) and 9 other shells (QVM:9:7855, 7856, 7858, 7860). For statistics of the regression lines see Table 2.

Additional nineteenth century materials examined included shells from the South Esk River (ex Petterd collection, QVM:9:7854); those at the top of the box resembled the type materials in being distinctly angular but not sharply keeled, whereas a second group of shells found at the bottom of the box, beneath the cottonwool, included some with an acute keel resembling that of *G. atkinsoni*.

Also collected in the last century were five shells (ZMB Moll. 18900), from Tasmania but without further detail, which were first reported by Clessin (1885) under *Planorbis brazieri*, his replacement name for *P. fragilis* Smith, 1883 (preoccupied). These shells (Fig. 4G,H,I) and the type materials of *G. meridionalis* appeared conspecific when compared side by side, being particularly similar in the obtuse to moderately acute angle situated a little towards the left side, and in the microsculpture of spiral striae and riblets.

Among the recently collected materials, the most closely topotypical specimens identifiable as *G. meridionalis* are from near Stanley (AMS C314279) in Circular Head. The smaller of the shells from near Stanley closely resembled the lectotype series from Circular Head in their degree of angulation and general form. Larger shells were more depressed and most were sharply keeled (Fig. 3J,K,L); maximum diameter was about 0.7mm greater than in the lectotype series. All the shells from Stanley had microsculpture of spiral striae and riblets, like the lectotype series. Some shells over the entire size range had oblique lamellae of periostracum on the peripheral angle, forming a fringe. Over the directly comparable part of the size ranges, data for whorls, (a/b) and depression angle from the Stanley sample plotted within or close to the distribution for the lectotype series (Figs. 5,6,7), while larger shells plotted close to the extrapolated regression line for the types. Thus the large shells in the Stanley sample appeared consistent in form with the allometric patterns of growth observed in the lectotype series; and therefore the larger, more depressed and sharply keeled shells are believed to be the fully grown form of the species represented by the types.

Shells from Lagoon of Islands (TMH E12333) (Figs. 4A-F, 8,9), the sample that provided most of the dissected animals, spanned the wide size range of 1.5 to 5.0mm diameter and reached nearly 4 whorls (Fig. 8). The flatness index (a/b) increased from 2.6 to about 5.4 over the size range (Fig. 9); although the periphery tended to become increasingly angular with shell size, there was wide variation in shells of similar size (Figs 4B,E; 10). The smallest shell with a distinct keel was only 2mm in diameter, but a keel was most frequent in large shells over 4mm diameter. Microsculpture like that in the type materials, consisting of spiral rows of striae and riblets. Some shells had a distinct fringe. Although some of the shells from Lagoon of Islands closely resembled the type materials in general appearance, many were more acutely angled and the inner whorls were less sunken on the left side. A few of the more acutely angled specimens had the lip deflected towards the right side in the manner of *G. atkinsoni*. However, the similar distributions of shells from Lagoon of Islands and shells of corresponding size among the type materials, in plots of whorl number (Fig. 8) and a/b (Fig. 9), suggests that the two sets of shells are conspecific. The larger shells from Lagoon of Islands are nearly one mm greater in diameter and have about half a whorl more than the biggest paralectotype of

G. meridionalis. The allometric trend for the degree of depression to increase with size results in large shells from Lagoon of Islands giving high values for a/b of up to 5.15 (Fig. 9), overlapping the distribution for large shells of *G. atkinsoni*. It seems likely that this degree of depression would have been seen in the lectotype series from Circular Head if any of these shells had grown to such a size.

In other samples the shells conformed to the range of form shown by the type materials and the samples from Stanley and Lagoon of Islands. A maximum diameter of about 5mm was attained by specimens from Lake Tiberias (AMS C314271) and Lake Crescent (AMS C314278). These large shells like those from Stanley and Lagoon of Islands were depressed and most were acutely angled; a few had the peripheral situated towards the right side and thus approached the form of *G. atkinsoni* (see below). This form was possibly represented by strongly keeled shells from Lake Leake (TMH E2406), but these were too much decalcified to be sure. The angulation of the shells from Marys Puddle (QVM:9:11334) was comparatively obtuse and like the shape in the series representing *G.tasmanicus*.

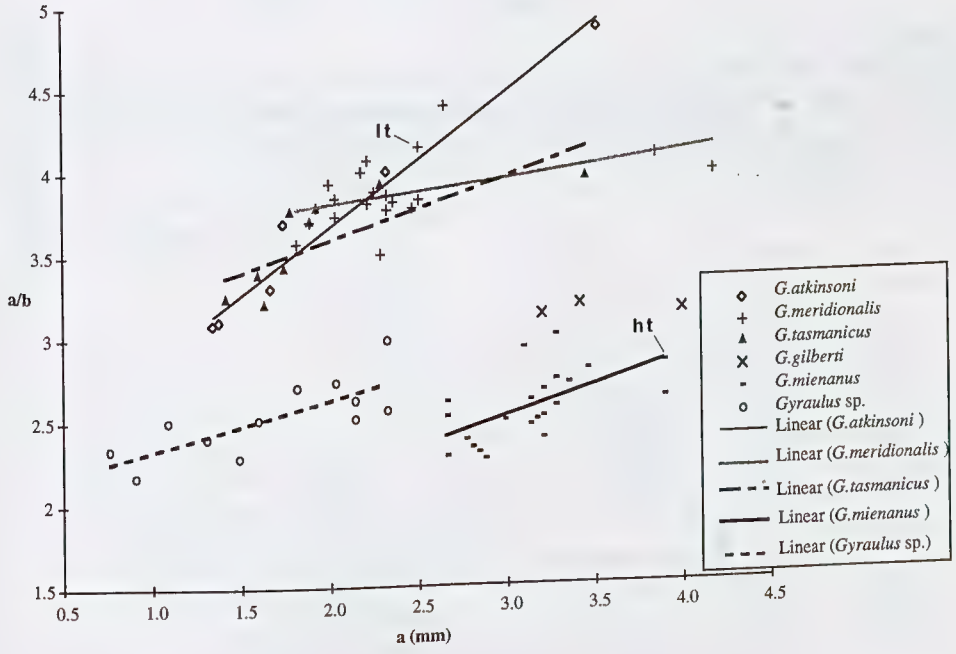

Figure 6.
Flatness index (a/b) plotted against (a) for shells of *Gyraulus*. *G. atkinsoni:* 6 possible syntypes, TMH E879. *G. meridionalis:* lectotype (lt), 19 paralectotypes from Circular Head (a few values are coincident), and two paralectotypes from Ouse River (QVM:9:116) isolated at righthand side of distribution. *G. tasmanicus:* 10 specimens, probable type material (TMH E872) (a few values are coincident). *G. mienanus* sp.n.: holotype (ht), 13 paratypes (QVM:9:7857, 7862). and 9 other shells (QVM:9:7855, 7856, 7858, 7860 and 7862). *G. gilberti:* 3 syntypes. *Gyraulus* sp.: 12 shells from Lake Sorell, AMS 314276. For statistics of the regression lines see Table 2 .

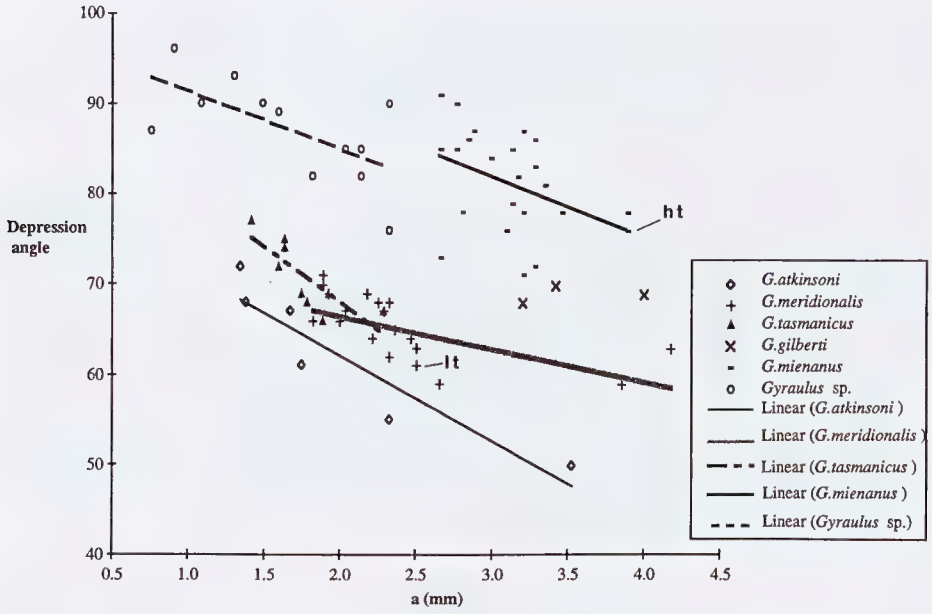

Figure 7.
Depression angle (DEP) plotted against (a) for shells of *Gyraulus*. Taxa, specimens and symbols as in Fig. 6. For statistics of the regression lines see Table 2.

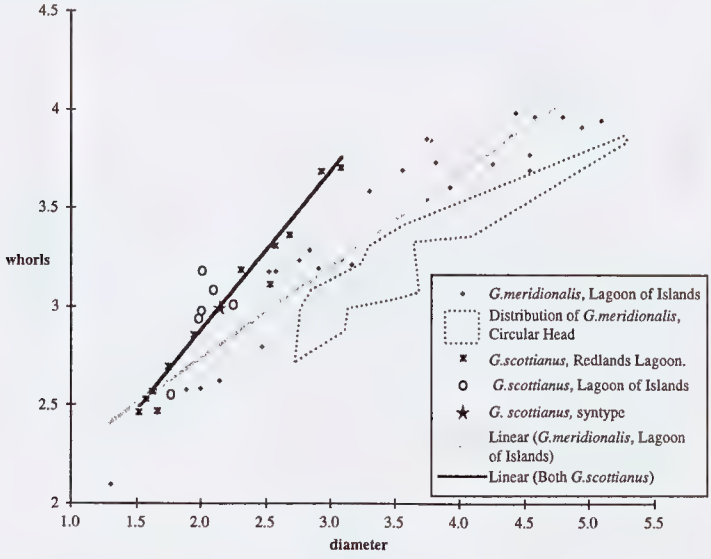

Figure 8.
Number of whorls plotted against shell diameter for shells of *Gyraulus*. *G. meridionalis* from Lagoon of Islands,TMH E12333, selected to represent the size range (n=29). *G. meridionalis*, polygon representing the distribution of the lectotype material (Circular head, AMS 100598) plotted in Fig. 5. *G. scottianus:* from Lagoon of Islands, TMH E12333 (n=6), Redlands Lagoon, TMH E9991 (n=12) and syntype, SMA D16180. For statistics of the regression lines see Table 2.

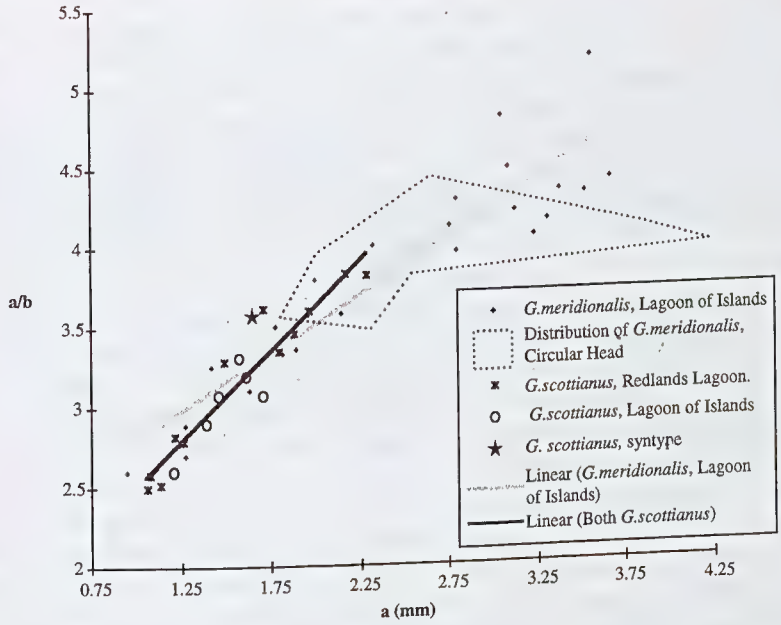

Figure 9.
Flatness index (a/b) plotted against (a) for shells of *Gyraulus*. *G. meridionalis* from Lagoon of Islands (TMH E12333), selected to represent the size range (n=27, some values coinciding). *G. meridionalis*, polygon representing the distribution of the lectotype materials plotted in Fig. 6. *G. scottianus* Lagoon of Islands (TMH E12333, n = 6), Redlands Lagoon (TMH E9991) and syntype, SAM D16180. For statistics of the regression lines see Table 2.

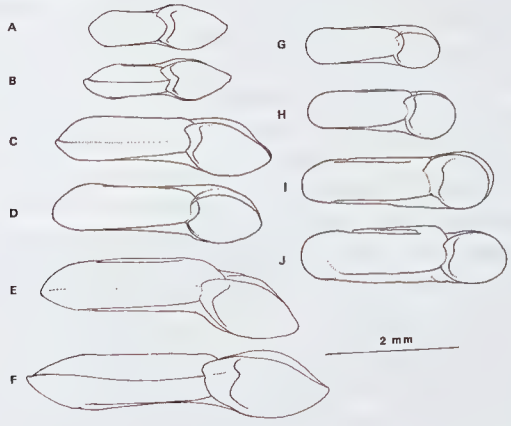

Figure 10.
Shape of shell periphery. **(a-f)**, *G. meridionalis* from Lagoon of Islands, small to medium-sized specimens. **(g-j)**, *G. scottianus* from Lagoon of Islands **(g,h)** and Redlands Lagoon **(i,j)**, medium to large specimens. In *G. meridionalis* the degree of angulation varied widely regardless of size, but all the shells were at least subangled, with a distinct keel present in some specimens over the whole size range. In contrast, *G. scottianus* was always more or less evenly curved.

Anatomy (Figs 11-15, 16K,L): Five specimens from near Stanley (AMS C314279) were dissected; all the bodies were retracted to about one-quarter of a whorl from the aperture and three had evident parasitic infections which had severely damaged some organs. A larger sample of 14 snails from Lagoon of Islands (TMH E12333) was also dissected; these bodies were retracted up to one-third of a whorl and three carried trematode infections that had severely damaged some organs. Morphological data for snails from Lagoon of Islands are summarised in Table 3; specimens from Stanley differed only in weaker pigmentation, which was scarcely evident in some. In the Lagoon of Islands sample, head/foot diffusely greyish black, mantle roof (Fig. 11A) with a dark band along the border and scattered dark granules concentrated along the margins of the kidney and above the uterus, but not forming a distinct pattern. Melanin more dense internally, around the stomach and intestine, which sometimes were conspicuously black. Kidney margins straight or if somewhat undulating this seemed due to contraction. Intestine straight or deflected posteriorly to some extent, varying from a small kink to a posterior loop reaching the stomach (Fig. 11B). Copulatory organ (Figs 11C,D; 12, 13) nearly 2mm long at shell diameter 5mm; about half its length contributed by the penis sheath, of which the proximal end is rounded and strongly muscular, with the vas deferens inserted a little to one side. At shell diameter 2.6mm the copulatory organ is about 1.2mm long (Fig. 18K,L), about twice as long as in *G. scottianus* at this diameter. Penis short and stout, the attachment of its base within the penis sheath situated between one-third and one-half of the distance from the proximal end of the sheath towards the preputium, and indicated by a low ridge on the external surface of the sheath (Fig. 12A, 13A). This condition contrasts with the more proximal attachment of the penis in *G. gilberti* of mainland Australia (Fig. 12C). Penis tip swollen and glans-like (Fig. 13B), with a chitinous stylet of the dagger-like type; stylet blade shorter and broader in proportion to its base than in *G. scottianus* (Fig. 12E). Penial opening situated close to the tip and connected by a groove to the base of the stylet, as figured for other species (Meier-Brook, 1983, e.g. fig. 45). Prostate gland (Fig. 11C, 14A) with up to 15 main lobes; possibly all borne on a separate prostatic duct, though only a few proximal lobes were readily separable from the sperm duct by dissection (all the lobes arose from a separate prostatic duct in an animal from Lake Crescent ,see below). Bursa copulatrix (Fig. 14B) varying in shape from club elongate to tadpole spherical. Seminal vesicle usually with about 6 spinous convolutions, but smooth in one specimen (Fig. 14C). Ovotestis lobes indistinct, up to 22, in approximately two rows. Radula (5 from snails of diameter about 4.7mm): maximum dimensions of ribbon, 1.10 x 0.17mm; formula (18-23)-1-(18-23); number of transverse rows about 200. Central tooth bicuspid, cusps pointed; inner lateral teeth with 3 main cusps, all slender and pointed, the endocone and ectocone nearly half the length of the mesocone; apparently at least one small additional cusp low on the lateral side of the inner lateral teeth and two or three such cusps on teeth near the margin of the radula.

Other material dissected comprised 4 specimens from Marys Puddle (QVM:9:11334), of which the shell resembled representative shells of *G. tasmanicus* (see also under that species), and 12 specimens from 5 other localities:

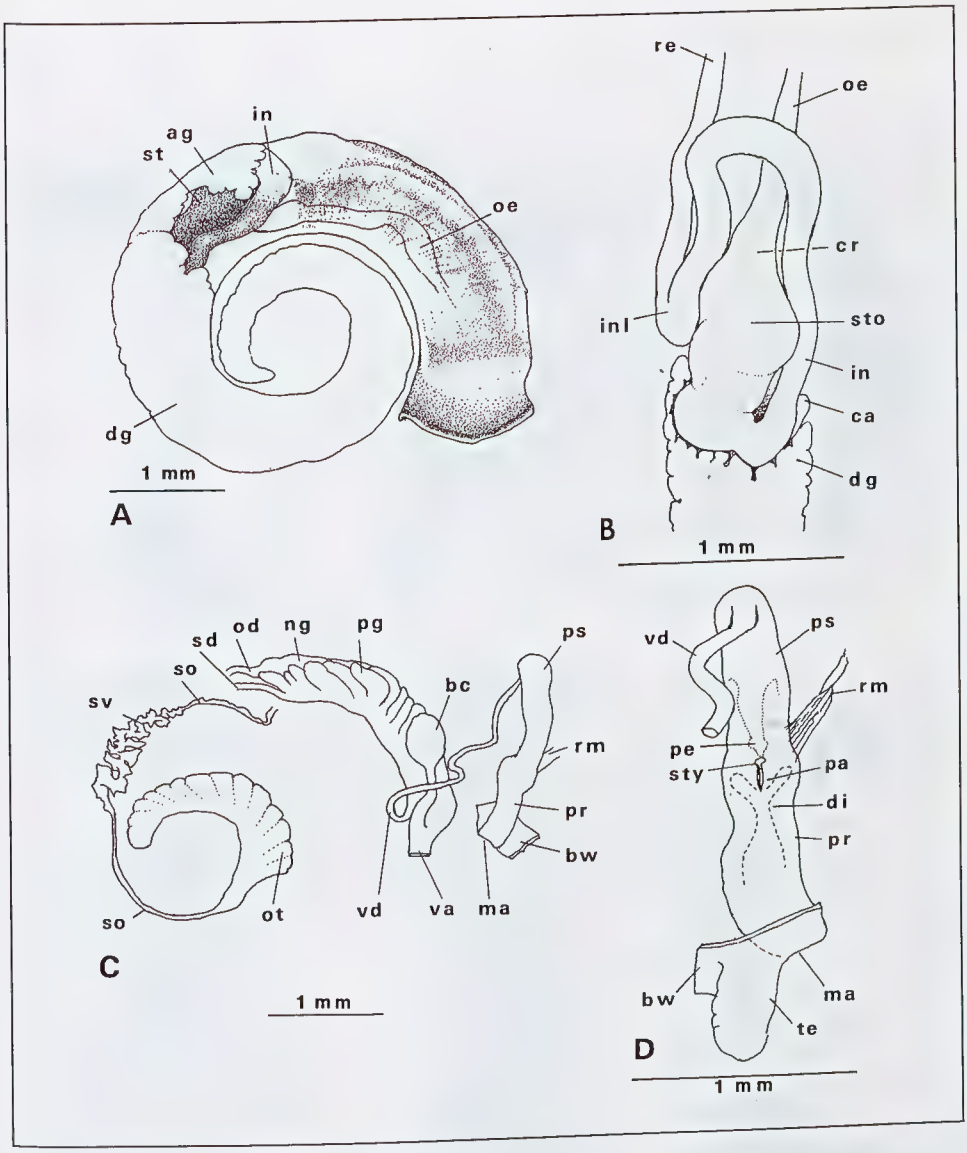

Figure 11.
Gyraulus meridionalis from Lagoon of Islands. **A**, body viewed from right side, showing diffuse pigmentation on mantle roof and the denser pigmentation on stomach and intestine. **B**, intestine, with posterior loop. **C**, genital organs viewed from right side (carrefour not shown). **D**, copulatory organ viewed from left side; broken lines indicate the penis and internal structure of the preputium. Labelling: **ag**, albumen gland. **bc**, bursa copulatrix. **bw**, body wall. **ca**, caecum. **cr**, crop. **dg**, digestive gland. **di**, diaphragm. **fa**, female aperture. **in**, intestine. **inl**, intestinal loop. **ma**, male aperture. **ng**, nidamental gland. **od**, oviduct. **oe**, oesaphagous. **ot**, ovotestis. **pa**, papilla. **pe**, penis. **pg**, prostate gland. **pga**, anterior part of prostate gland. **pp**, penis pore. **pr**, preputium. **ps**, penis sheath. **re**, rectum. **rm**, retractor muscle. **sd**, sperm duct. **so**, spermoviduct. **sod**, spermoviduct, distal part. **sop**, spermoviduct, proximal part. **st**, stomach. **sty**, stylet. **sv**, seminal vesicle. **te**, tentacle. **ut**, uterus. **va**, vagina. **vd**, vas deferens.

Figure 12.
Copulatory organs of *Gyraulus*. **A**, *G. meridionalis* from Tasmania, Stanley (AMS C314279). **B,F**, *G. meridionalis* from Tasmania, Lake Tiberias (AMS C314271). **C**, *G. gilberti* from New South Wales, Grafton (AMS C144815). **D,E**, *G. scottianus* from Tasmania, Lawrenny (TMH E9988). Labelling: **rm**, retractor muscle. **vd**, vas deferens. Arrows indicate position of attachment of the penis within the penis sheath. Scale lines represent 0.3mm (A-D, F) or 0.03mm (E).

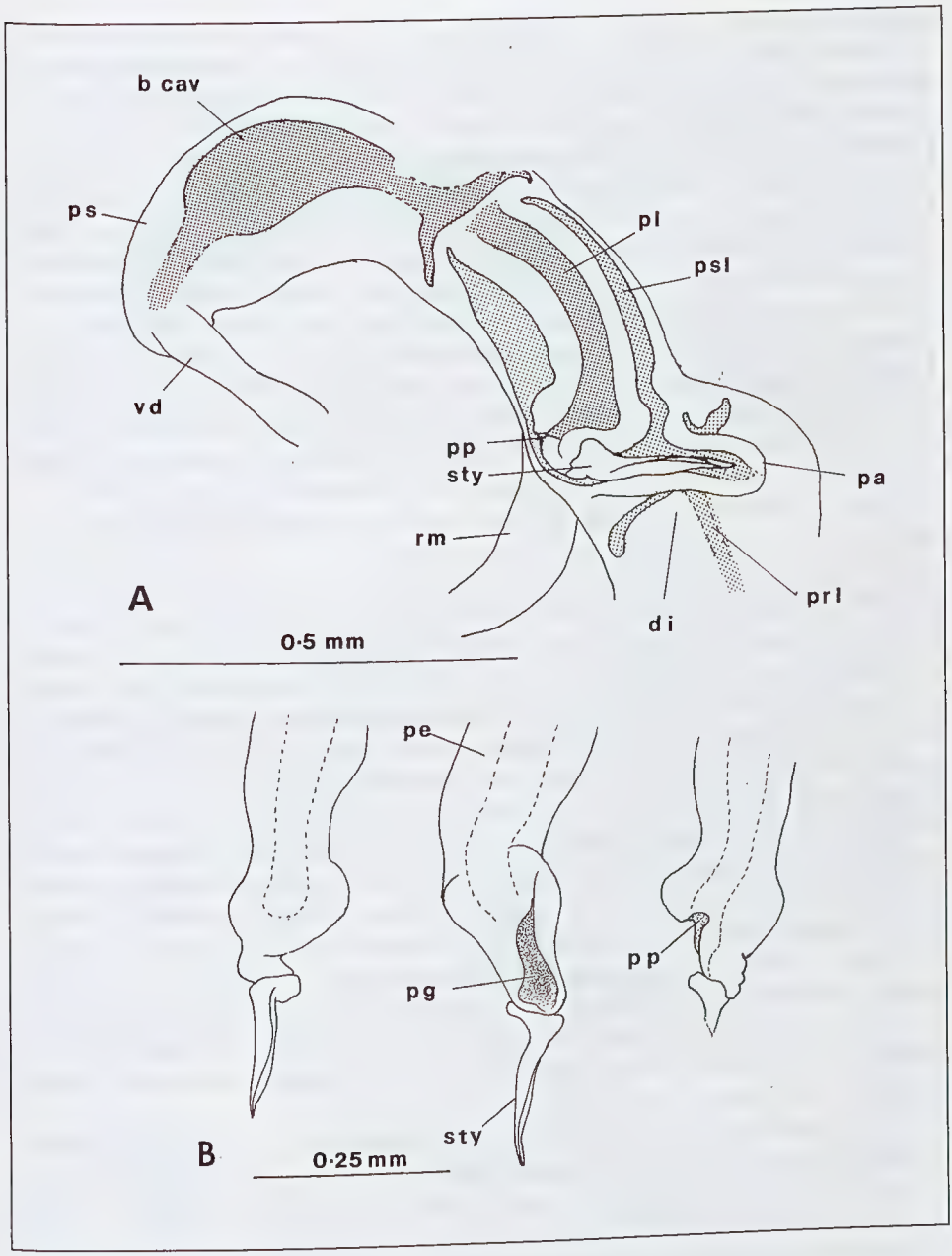

Figure 13.
Gyraulus meridionalis. **A**, upper part of copulatory organ of specimen from Stanley (AMS C314279), drawn to scale from permanent mount. Semi-diagrammatic representation of the internal structure. The stylet lies within the papilla, which is projecting through the diaphragm. Same specimen as shown in Fig. 12A, image reversed here. **B**, penis tips of 3 specimens from Lagoon of Islands, in different positions; the stylet of the one on the right is incomplete. Labelling: **b cav**, bulbous cavity. **br cav**, broad cavity at base of penis. **di**, diaphragm. **pa**, papilla. **pe**, penis. **pgr**, penial groove. **pl**, penis lumen. **pp**, penis pore. **ps**, penis sheath. **ps l**, penis sheath lumen. **pr l**, preputium lumen. **rm**, retractor muscle. **sty**, stylet. **vd**, vas deferens.

AMS C314271, -273, -277, -278; TMH E2406. These specimens were anatomically similar to those from Stanley and Lagoon of Islands; of particular interest is the uniformity in the attachment of the penis far from the end of the sheath (e.g. example from Lake Tiberias, Fig. 12B) and in the form of the stylet ((Fig. 12F). Pigmentation varied from being almost undetectable apart from the eye spots, to the condition described for the Lagoon of Islands sample. An additional feature was the presence in most of the snails from Pipers Lagoon Creek (AMS C314273) of a patch of orange-brown granules, visible through the shell wall, situated on the mantle roof and medially between the distal end of the kidney and the mantle margin. In an exceptionally well preserved animal from Lake Crescent (AMS C314278) the prostate lobes and duct were entirely separable from the sperm duct, and a few well-defined septa were evident in the kidney (Fig. 15A,B). Radula (QVM:9:11334, Marys Puddle; 2 from snails of diameter 3.1 and 3.9mm); formula 20-1-20 and 22-l-22; maximum dimensions of ribbon 0.80mm x 0.16mm; number of transverse rows about 170.

Anatomical characters of *G. meridionalis* are compared with other taxa in Table 4.

Remarks: Brazier's description of the shell corresponds adequately to the lectotype series from Circular Head (AMS C100598), despite some apparent discrepancies. Today these shells would hardly be described as "sharply carinated", but when Brazier was writing none of the more acutely angled and keeled of the Australian species had been described (e.g. *P. atkinsoni*). The larger and apparently conspecific specimens from near Stanley (AMS C314279) are distinctly keeled. Brazier's count of only 3 whorls (about one-third of a whorl less than measured here) and his failure to describe any spiral sculpture can be explained by the fact that the shells were not adequately cleaned (in order to examine these features properly I had to remove thickly encrusting reddish-brown material from most specimens). The shell diameter given by Brazier is 3.71mm (1 line = 2.12mm), and this corresponds reasonably well to my measurement of just over 4mm for the maximum diameter of the shells from Circular Head. However, the paralectotypes from the Ouse River are considerably larger; the one intact shell measured 5.27mm in diameter and the damaged specimen was even bigger.

I have chosen the lectotype from the syntypes from Circular Head (AMS), since their provenance is well supported by the presence of old labels indicating that these shells are from Brazier's collection and are "author's type". According to the asterisk symbol in Brazier's description (explained in the footnote to p. 17 of his paper), specimens were deposited in the cabinet of the Linnean Society of New South Wales; from there they could have been transferred to the Australian Museum. The origin of the two paralectotypes from the Ouse River (QVM:9:116, "syntypes"), is less clear. It is surprising that their large size was not mentioned by Brazier. Further, there is no label with these shells to indicate that they were received from Brazier, and Petterd (1889) referred to three, not two, type specimens sent to him by Brazier.

The selection here of a lectotype serves to restrict the type locality of *G. meridionalis* to Circular Head, which is a well-defined area, being the

peninsula where is situated the town of Stanley. Brazier did not specify any particular collection site in the Ouse River, which arises from Great Lake on the plateau at an altitude of above 1000m and flows about 80km southwards to its confluence with the Derwent River, below 200m. Petterd (1889) followed by May (1921a) gave the type locality as the Upper Ouse River; neither provided a reason for doing this. The recently collected material from near Stanley clearly has a strong claim to be regarded as topotypical, while the specimens from closest to the Ouse River are from Lagoon of Islands, situated about 12km from the river at about 900m altitude.

Planorbis meridionalis Brazier, 1875 is an important taxon in the classification of Australian species of *Gyraulus*, as it is pre-dated only by *P. gilberti* Dunker, 1848, of "New Holland". The syntypes of *gilberti* (BMNH 1969146) are not much separated from *meridionalis* in plots of whorl number (Fig. 5), but they are clearly separated in plots of the flatness index (Fig. 6) and depression angle (Fig. 7).

Confusion arose early as to the nature of Brazier's species, beginning with the first subsequent account, by Petterd (1889), who presented the first figure of a shell, which he stated was from the Ouse River and one of "the three type specimens" sent to him by Brazier. Petterd did not mention Circular Head as a locality, and said he had seen it only from the Upper Ouse River and Great Lake. Petterd's figure does not match either of the supposed syntypes from his collection (QVM:9:116) and nor does it correspond at all well with Brazier's description or the syntypes from Circular Head. The figured shell is larger (according to the accompanying scale its diameter is at least 5mm), distinctly angular above and below a peripheral keel (which is the only angle mentioned by Brazier) and has conspicuous transverse ridges (Brazier described only faint lines of growth). The appearance of this shell is unusual for *Gyraulus* and I was puzzled by it for many years, having seen nothing like it among many specimens from mainland Australia. In 1995 I found similar shells in a collection loaned to me from the Queen Victoria Museum, Launceston (through the courtesy of Dr Brian Smith). There were 6 lots of such shells, including some from Petterd's collection; all were collected from Great Lake and they differ from any species previously described from Australia (see *Gyraulus mienanus* sp. n., present paper).

Perhaps Petterd confused shells from Great Lake with examples of *meridionalis* sent to him by Brazier, or possibly Brazier had sent him shells from the lake by mistake. In any case Petterd's account shows that he considered angular shells from Great Lake to be *meridionalis*, but at the same time he seems to have recognised their distinctive appearance, since he cited as a synonym his manuscript name *P. cathcarti*, given to specimens from Great Lake (see under *G. mienanus* sp. n.).

The next published figure of *Planorbis meridionalis* was "from Petterd's co-type" (May, 1921a, pl. 10, fig. 11) and represents what appears to be the one shell still intact of the two paralectotypes from the Ouse River (QVM:9:116). It is surprising that May did not remark on differences between this shell and the figure of *meridionalis* by Petterd, but probably May did not give this much attention, as he says of Brazier's figures (p. 67):"many of these, however,

especially of the smaller species are very roughly executed, and are of little value for identification."

Iredale (1943) listed *meridionalis* as a species in his newly named *Glyptanisus*, with *Planorbis cathcarti* Petterd, 1889 as a synonym. Iredale cited May (1921a, pl. 10, fig. 11) under *P. cathcarti*, but as we have seen above this figure represents a shell different from shells from Petterd's collection that are labelled *cathcarti* (see also under *G. mienanus* sp. n.).

Another figure of *G. meridionalis* was published by Cotton (1943, as *Glyptanisus*), with the locality South Tasmania (in the text). This shell is high in proportion to its breadth, with a widely expanded lip, and shows some resemblance to the distinctive form found in Great Lake. Cotton certainly had shells from the lake, since he figures one stated to be from there as a variant of *Glyptanisus atkinsoni*.

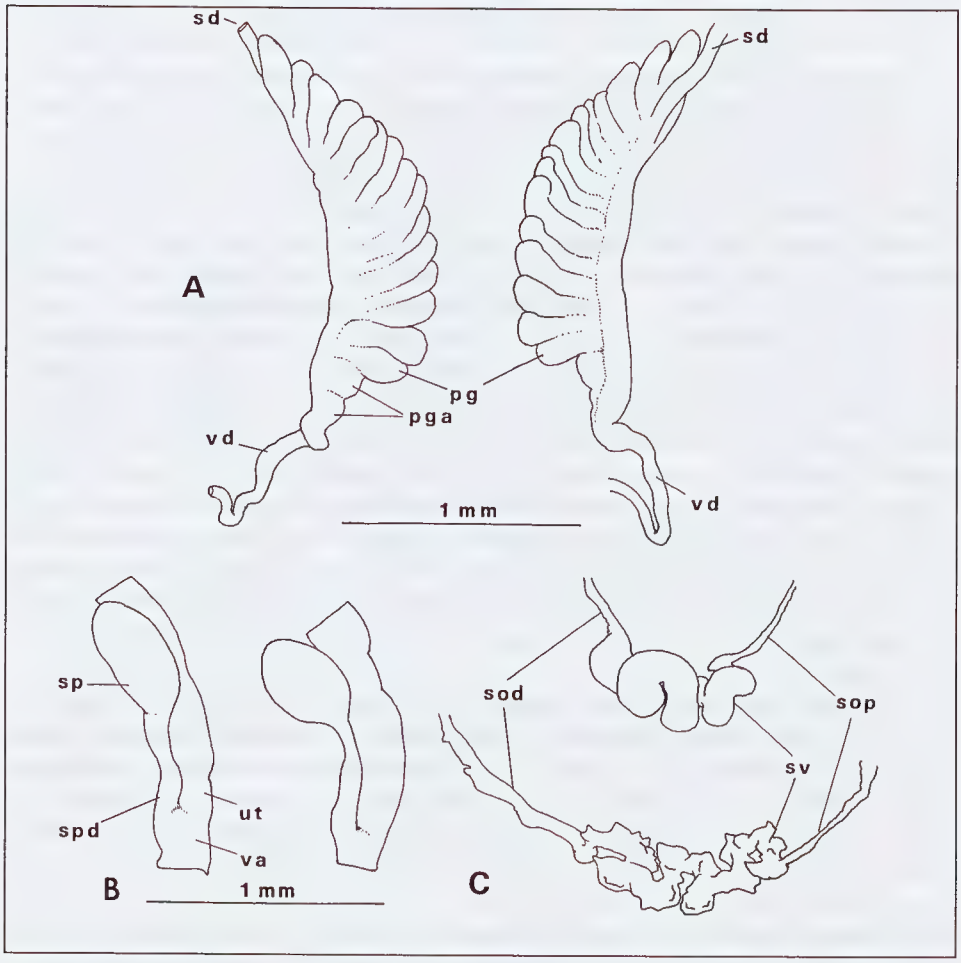

Figure 14.
Gyraulus meridionalis from Lagoon of Islands. **A**, prostate gland viewed from right side and left side. **B**, bursa copulatrix from two specimens. **C**, seminal vesicle from two specimens (the upper one being the only non-spinous example seen). Labelling as in Fig. 11.

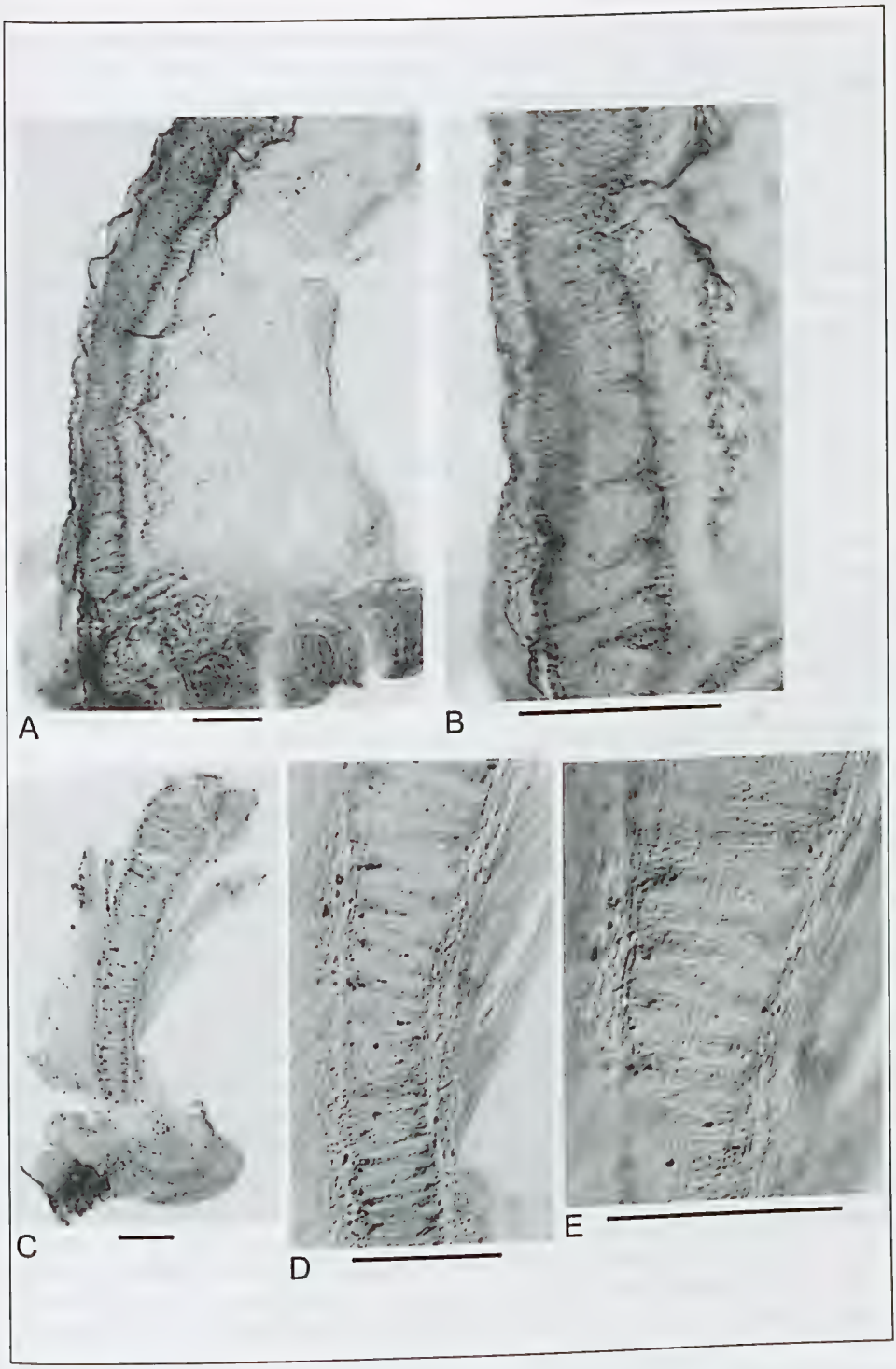

Figure 15.
Kidneys of *Gyraulus*. **A,B**, *G. meridionalis* from Lake Crescent (AMS C314278). **C-E**, *G. scottianus* from Lagoon of Islands (TMH E12333). Scale lines represent 0.2mm.

We may conclude that *Planorbis meridionalis* Brazier has been misunderstood by some authors. The locality Circular Head (part of the collective type-locality) and syntypes from there were ignored by both Petterd (1889) and May (1921a), and they introduced Great Lake as a locality. The first figured example of *meridionalis* (Petterd, 1889) appears to have come from this lake, as this shell has the distinctive form here described as a new species. Smith & Kershaw (1981) followed Petterd's broad concept of *Gyraulus meridionalis*; they figure a depressed and sharply keeled shell, while their distribution map shows localities apparently in Great Lake and thus presumably representing populations of *G. mienanus* sp. n. According to Smith & Kershaw (1979) *G. meridionalis* occurs throughout the south eastern mainland of Australia as well as Tasmania, but the taxonomic relationships between the *Gyraulus* faunas of these two areas are not yet clear (see Discussion).

Gyraulus tasmanicus (Tenison-Woods, 1876)
(Figs 4J,K,L; 5,6,7)

Planorbis tasmanicus Tenison-Woods, 1876: 79; 1879: 69; - Johnston, 1879: 26, 28; 1889: fig. 6 in third page of figs between pp 86-87 (see Remarks below); - Tate & Brazier, 1882: 599; - Petterd, 1889: 68, pl. 2, figs 8 and 9; - Johnston, 1891: 145; - May, 1921a: 70, pl. 10, figs 13 and 14; 1921b: 90; 1923, pl. 41, 19; Gabriel, 1939: 121-122, pl. 3, fig. 27.
Plananisus tasmanicus - Iredale, 1943: 255.
Pygmaniscus [sic] *tasmanicus* - May & Macpherson, 1958: pl. 41, 19.
Gyraulus tasmanicus - Smith & Kershaw, 1979: 88 with fig.; 1981: 61 with fig.; Smith, 1992: 270.

Original description: (English version in Tenison-Woods) "Shell discoidal, minute, flattened, thin, convex above, umbilicate below, thickly sinuately striate, shining pellucid, pale horny; whorls 4 to 4½, convex, dilated at the base, suture deep, aperture ovate, oblique, peristome simple, sinuated. Diam. 5, base 3½, height 1mill. Habitat, still waters throughout the island."

Representative materials examined: Tasmania, TMH E872 (10 dry and computer images of a further 9 specimens retained at the Tasmanian Museum). Selected early in the present century as probable type material (see under Remarks). QVM:9:7865 (5 dry) Circular Head, ex Petterd collection, original identification *P. tasmanicus*.

Description of representative shells (see above) (Figs. 4J-L, 5, 6, 7, Table 2): The largest specimen in lot TMH E872 is broken and was about 5.25mm in diameter. These shells resemble the lectotype series of *G. meridionalis* in number of whorls (Fig. 5), flatness index (a/b from 3.21 to 3.96, Fig. 6) and depression angle (Fig. 7). Periphery of varied shape, from an almost even curve to an angle nearly as acute as in the most angular of the lectotypes of *meridionalis*, but not distinctly keeled and not fringed. Whorls 1-3 slightly sunk on the right side, which is nearly flat. Left side concave, the last whorl embracing the earlier ones deeply;

surface of last whorl generally evenly curved, becoming flatter towards the lip in some specimens. Microsculpture weaker than in the types of *meridionalis*, though similarly consisting of numerous fine transverse ridges subdivided by spiral striae.

Dimensions of probable type material (TMH E872):

	whorls	diameter	a	b	a/b
largest (damaged, whorls and diameter estimated)	3.80	5.25	3.46	0.87	3.96
largest complete shell	3.23	3.42	2.29	0.58	3.93
smallest	2.83	2.26	1.42	0.44	3.25

Some of the shells from the Petterd collection identified as *P. tasmanicus* (QVM:9:7865) have a more acute peripheral angle than any in lot TMH E872 and are keeled.

Anatomy: The dissected specimens (QVM:9:11334) had shells similar to the representative specimens (TMH E872) and anatomical observations are given under *G. meridionalis*. The soft parts, including the copulatory organ, showed no differences from even the most depressed and sharply keeled examples of *meridionalis*.

Remarks: Planorbis tasmanicus Tenison-Woods, 1876 is the second oldest species-group name available for a Tasmanian species of *Gyraulus*, and it is the type of *Plananisus* Iredale, 1943. Tenison-Woods did not compare *tasmanicus* with any other species, and he later wrote (Tenison-Woods, 1879) that he had then been unaware of the description of *P. meridionalis* Brazier, 1875, of which he believed his species to be a junior synonym. This view seems correct.

No undoubted type of *tasmanicus* is known, but a series of 19 shells (TMH E872) was selected as probable type material by local conchologists early in the present century (Elizabeth Turner, in litt to DSB, 1995). These shells conform to Tenison-Woods' concept of this species, so far as can be judged from his brief original description. Although this does not mention a peripheral angle, which is present in some of the selected shells, Tenison-Woods (1879; 69, 72) does not appear to have had any doubt that his species was the same as *Planorbis meridionalis*, described by Brazier as "sharply carinated at the periphery". The words "thickly sinuately striate" in Tenison-Woods' English description of *tasmanicus* do not mean that the sculpture is strong, but that the sculptural elements are set close together (from *confertim* in the Latin version).

Although the origin of *P. tasmanicus* was given by Tenison-Woods simply as throughout Tasmania, Smith (1992) limited it to Circular Head, though following early authors. Johnston (1879) was the first to record Circular Head; Petterd (1889) added the South Esk and Liffey rivers, but May (1921a) mentioned only swamps at Circular Head. According to Smith & Kershaw (1981) *G. tasmanicus* is most common in the northern part of Tasmania.

Johnston (1879) stated that he had received specimens of *P. tasmanicus* from Circular Head that were mostly slightly keeled (p. 26), with a slightly angled aperture (p. 28). He later figured a shell (Johnston, 1889, pl. 2, fig. 6), without figure legend, but which apparently represents this species (these figures are discussed here under *G. atkinsoni*). Although drawn crudely, this shell is clearly depressed with an angular periphery, and in general form resembles the probable type material (TMH E872). Petterd (1889) provided a somewhat better drawing, showing a depressed shell with a blunt peripheral angle and an almost evenly curved outer lip. He reported collecting *tasmanicus* in abundance from pools and marshes at Circular Head, and occasionally in the South Esk River near Launceston. Petterd was unaware, or at least did not mention it, that Circular Head had been given as a locality for *P. meridionalis* by Brazier (1875).

Petterd (1889) commented that *tasmanicus* "is but obscurely angled below the periphery", whereas he wrote of *meridionalis* "sharply carinated periphery". Petterd's opinion that *tasmanicus* was "totally distinct" from *meridionalis* was presumably influenced by his belief that the latter was represented by shells from Great Lake, but these belong to a different species (see under *meridionalis* and *G. mienanus* sp.n.). Two shells "compared with the type series" were figured by May (1921a), the smaller one being closely similar to some in the probable type materials (TMH E872), the larger one having a more expanded aperture. May did not comment on differences between *tasmanicus* and *meridionalis*, but maintained them as distinct consistently (May, 1921a, 1921b, 1923; May & Macpherson, 1958).

G. tasmanicus continued to be regarded as a distinct species by Smith & Kershaw (1979, 1981), described as keeled but less sharply so than *meridionalis*. These authors' figures (the same in both publications) show a definite keel in the latter species, and a distinctly projecting peripheral angle in *tasmanicus*. According to Smith & Kershaw (1981) *G. tasmanicus* is present in eastern and central Victoria, and southern NSW as well as Tasmania. In an earlier description of this species based on snails collected in Victoria State, Gabriel (1939) had remarked on "considerable variation in the sharpness and position of the keel".

When Iredale (1943) selected *tasmanicus* to typify his new genus *Plananisus*, characterised partly by rounded whorls, he seems to have had in mind the larger of the two shells figured by May (1921a fig. 12). But a distinct angle had been shown in the figures by Johnston (1889) and Petterd (1889), and there is one in most of the representative shells (TMH E872) described here.

In comparison with the lectotype series of *G. meridionalis* from Circular Head the only differences observed in the probable type materials of *G. tasmanicus* (TMH E872) were that their microsculpture was generally weaker and that the peripheral angle was less acute that in some specimens of *meridionalis*. But the combined values for the flatness index (a/b) and for the depression angle gave continuous intermingling distributions (Figs 6,7) and it may be emphasised that angulation was evident on at least a part of the periphery of all the shells representing *tasmanicus*. Since no difference from *meridionalis* was observed in the soft parts, it does not seem justifiable to maintain *tasmanicus* as a distinct species.

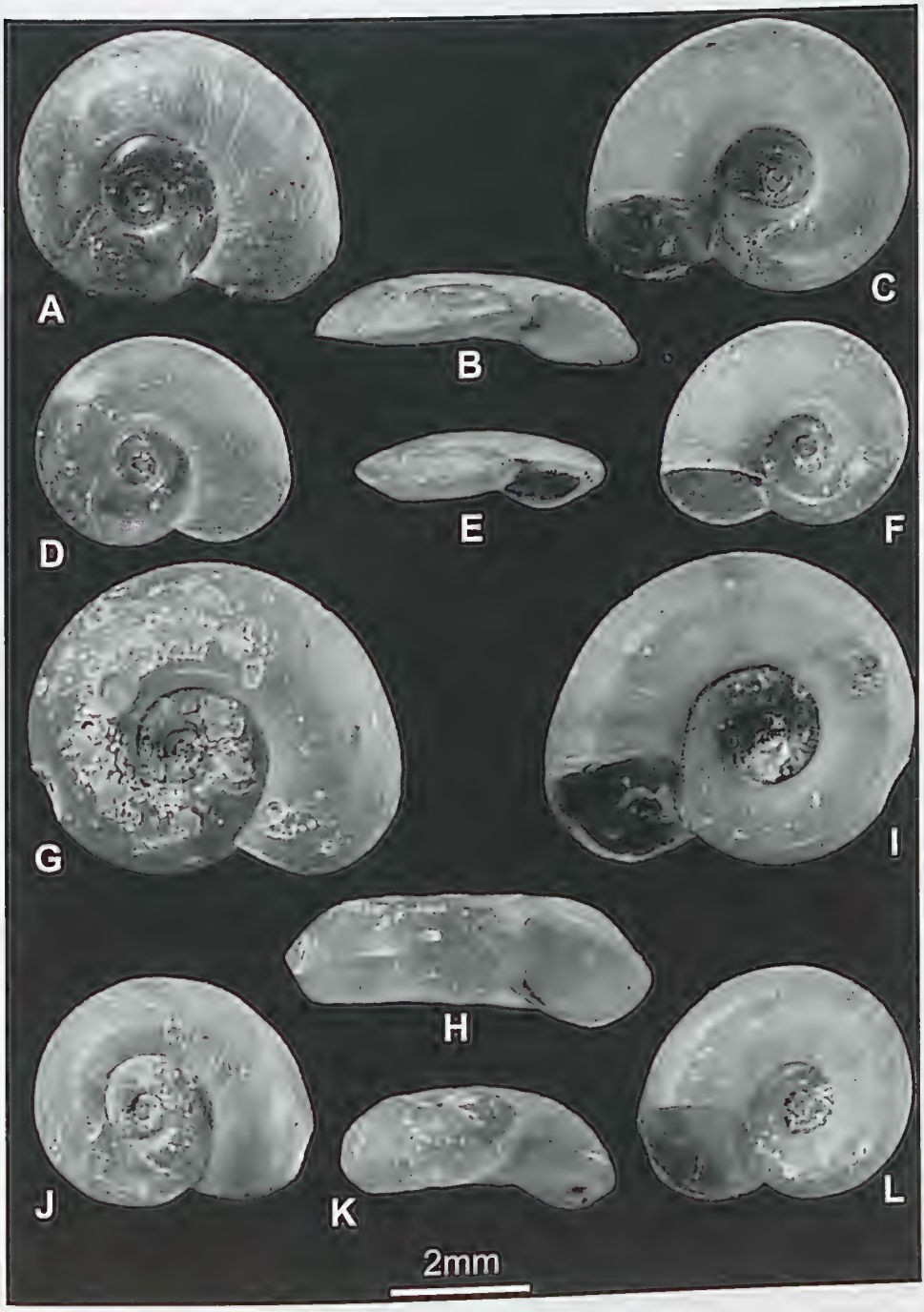

Figure 16.
Shells of *Gyraulus*. **A-F**, *G. atkinsoni*. **A,B,C;** possible syntype, from South Esk River (TMH E879). **D,E,F;** early example, from Epping, ex Petterd collection (QVM;9:7864). **G-L**, *G. mienanus* sp.n., from Great Lake. **G,H,I;** holotype and **J,K,L;** paratype (QVM:9:7857).

Gyraulus atkinsoni (Johnston, 1879)
(Figs 5,6,7,16A-F)

Planorbis atkinsoni Johnston, 1879: 26; 1889: 86, figs 5a-c in second sequence of figures; - Tate & Brazier, 1882: 559; - Petterd, 1889: 63, pl. 2, figs 6 and 7; - May, 1921a: 70 (in part, non pl. 10, fig. 10); 1921b: 90; 1923: (in part, non pl. 41, fig. 16); - Cotton & Godfrey, 1932: 162; - Smith, 1992: 277.
Glyptanisus atkinsoni - Iredale, 1943: 225 (not of May, 1921a, pl. 10, fig. 10); - Cotton, 1943: 148, pl. 19, figs. 1 and 2, non pl. 19, figs 3 and 4.
Glyptaniscus [sic] *atkinsoni* - May & Macpherson, 1958 (non pl. 41, fig. 16).

Original description: "Shell minute, irregularly flatly discoid, with an open shallow umbilicus, and sunken nucleus; whorls 4, angled, rapidly increasing, depressed; preceding whorls embraced, and slightly sunk in the last; last whorl flattened irregularly above, slightly convex below; somewhat obsoletely keeled above at abrupt expansion near suture, and constricted and sharply keeled at the periphery; surface finely, obliquely arcuately striate; aperture nearly two-thirds of the breadth of shell, obliquely and narrowly cordate-acuminate, with channel formed by the sharply keeled periphery, and two grooves anteriorly and posteriorly formed by the projecting keel of preceding whorl; margins simple, approaching, and obliquely connected by a more or less distinct callus; upper margin obliquely produced. Diam., max. 5, min. $3^1/_2$, alt. 1 [no units given]. Habitat, common on leaves of Triglochin, South Esk, from Avoca to Launceston."

Representative materials examined: TMH E879 (9 dry). South Esk River, with old label "Planorbis atkinsoni R.M.J., So. Esk, Tas" [presumably from the collection of R.M. Johnston]. Possibly these are syntypes (see under Remarks).

Additional materials examined: BMNH 93.3.2.372-7 (6 dry). Sth Esk, Clynevale, J.H. Ponsonby. BMNH without reg. No. (3 dry). Travallyn, ded. W.F. Petterd ex A.S. Kennard colln. QVM:9:7859 (3 dry). South Esk, Clynevale; also labelled "Epping". QVM:9:7863 (13 dry). Epping, Simson collection; also labelled "Sth Esk, Clynevale, 1877". QVM:9:7864 (4 dry). Epping, Petterd collection; also labelled "*Planorbis atkinsoni* Johnston, Clynevale, South Esk River". QVM:9:7866 (3 dry). Tasmania; no further detail. QVM:9:10667 (10 dry). Dry bed of Jordan River near Apsley, 1956, R.C. Kershaw. QVM:9:11320 (5 wet). Bowlers Lagoon, EQ787759, 14 July 1994, McGowan and La Palombara, site 1. QVM:9:11331 (7 wet). As above, site 3. TMH E4344 (1 dry). South Esk River. AMS C144851 (2 dry). South Esk River at Evandale, in river and pools on side, 17 March 1975, W.F. Ponder & R.C. Kershaw.

Shell (Figs 5,6,7,16A-F, Table 2): Possible syntypes (TMH E879) have a maximum diameter of about 5mm and are depressed with a peripheral angle situated about medially or more towards the right side (Fig. 16A-C). Maximum diameter about 5mm (largest and broken shell), with 3.7 whorls (Fig. 5). Whorls low in proportion to their breadth, giving values for a/b of from 3.04 (smallest shell) to

4.97 (largest intact shell); the latter value is considerably higher than for any shell in the other taxa plotted in Fig. 6. Depression angle (Fig. 7), 50° to 72°. The larger shells have a strong keel, accentuated by the concavity of the whorl surface on either side. The keel is formed partly by thickening of the shell wall and partly by outward expansion of the wall, resulting in an internal channel; several shells have a fringe. Whorls 1 and 2 on the right side slightly sunken; after rising from the suture in a strong curve ('obsoletely keeled', Johnston) the whorl slopes almost flatly towards the periphery and then becomes a little concave near the keel. On the left side the inner whorls are more deeply sunken; surface of the last whorl strongly curved near the suture, but flat or slightly concave towards the periphery. Aperture broad and depressed; lip obtusely to acutely angular at the periphery, with an internal channel visible within the keel. Microsculpture strongest on the left side, with numerous fine transverse ridges divided into riblets by spiral striae. One of the possible syntypes has the keel close to the right side of the shell, and the last whorl slopes increasingly towards the right side as it approaches the aperture. This manner of growth has the effect, increased by some damage to the sinuous right side of the lip, of giving the aperture a hooked appearance, like the shell figured by Johnston (1889).

Dimensions of possible syntypes; the 6 least damaged shells:

whorls	diameter	a	b	a/b
3.70	4.87	3.53	0.73	4.97
3.09	3.67	2.33	0.53	4.00
2.84	2.73	1.75	0.47	3.69
2.76	2.58	1.67	0.51	3.25
2.69	2.11	1.38	0.44	3.10
2.52	2.04	1.35	0.44	3.04

The additional materials examined resembled the possible syntypes in size range and the strongly keeled periphery. An early example from Petterd's collection (QVM:9:7864) is shown in Fig. 16D-F. Measurements for dissected specimens are included in Figs 6 and 7.

Anatomy: Description based on 5 specimens from Bowlers Lagoon (QVM:9:11320 and 11331, the only material available for dissection). There were no evident differences from *G. meridionalis*. Pigmentation of head and anterior foot diffuse greyish-black; mantle with band of black along the anterior border; mantle otherwise unpigmented apart from scattered grey or black granules concentrated above the uterus and along the kidney. Kidney margins straight. Intestine with posterior loop extending back to stomach. Copulatory organ like that of *G. meridionalis* in size and structure though the penis tip was less swollen, perhaps due to the less contracted condition of the bodies. Prostate with 11 or 12 main lobes. Bursa copulatrix of elongate club shape (only one in good condition). Ovotestis with about 16 major lobes, in 2 approximate rows. Seminal vesicle with 6 to 8 spinous convolutions. Radula (2 specimens; QVM:9:11331); formula 21-1-21 and 22-1-22.

Remarks: G. atkinsoni is the third species of *Gyraulus* to be named from Tasmanian shells; it was placed by Smith & Kershaw (1979) in the synonymy of *G. meridionalis*. The example of *meridionalis* figured by Smith & Kershaw (1981) has a pronounced keel situated a little towards the abapertural side and thereby approaches the form of *atkinsoni*. However, *Planorbis atkinsoni* was later treated by Smith (1992) as a taxon incertae sedis "probably referable to *Gyraulus*", which it undoubtedly is by virtue of the anatomy described above.

No undoubted type of *P. atkinsoni* is known, but a series of shells from the South Esk River possibly are syntypes (TMH E879; Elizabeth Turner, in litt. to D.S.B., 1995). These correspond to Johnston's description (1879) of a shell form that is clearly recognisable among figures published later by Johnston (1889) and intended, he explained (p. 86), to accompany the earlier paper. These figures are sketchy and lack captions, but it can be deduced from the species mentioned in the text, that in the third page of figures one of the three planorbids (no. 5a-c) is *atkinsoni*, while no. 2a-c is *scottiana* and presumably 6a-c is *tasmanicus*, since this was the only other planorbid mentioned in the earlier paper.

Johnston's concept of *atkinsoni* was clearly of a depressed and strongly keeled shell; his figure shows a distinctive example having the keel close to the right side and with the expanded outer lip deflected towards the same side, appearing hook-shaped in apertural view. The next account of *atkinsoni* was by Petterd (1889), who figured a shell from the South Esk River, with the keel situated nearly at mid-whorl and the lip horizontal rather than deflected. Although Petterd's drawing suggests the presence of an angle on the left side of the last whorl, this is no more than strongly curved near the suture in examples seen by me. Petterd commented that the species was clearly distinct and found commonly on leaves of aquatic plants, sometimes in swiftly running water, plentifully at Clynevale.

Yet Petterd's collection was to become a source of confusion, as it did in the case of *Planorbis meridionalis*. A figure by May (1921a, pl. 10, fig. 10), he describes as "from Petterd's specimen compared with the type series", is much like the shells from Petterd's collection that are labelled *P. atkinsoni* but which came from Great Lake, and belong to *G. mienanus* sp.n. described in the present paper (e.g. QVM:9:7860). Other examples of this new species from Great Lake were misidentified as *P. atkinsoni*: QVM:9:7858 and 7862 from Simson's collection and a shell figured as a variant of *Glyptanisus atkinsoni* by Cotton (1943; the locality of Great Lake is given on p. 148). In the same paper Cotton figured as typical *atkinsoni* a smaller and more depressed shell, from the South Esk River (locality given on p.148) and more like Johnston's species.

The depressed, keeled form of shell described as *P. atkinsoni* seems connected by continuous variation to both *meridionalis* and *tasmanicus*, and possibly all these taxa are conspecific. No difference was observed in the soft parts of snails with the *atkinsoni* form of shell. However, the typical form of *atkinsoni* is so distinct that it seems justifiable to maintain the species as valid, at least for the present in order to encourage further study of its characteristics, distribution and ecology.

Gyraulus mienanus sp. n.
(Figs 5,6,7,16G-L)

Planorbis meridionalis Brazier, 1875 - Petterd, 1889: 63 (in part), pl. 1, figs 4-6 (non Brazier, 1875).
Glyptanisus meridionalis - Iredale, 1943: 225 (in part, see under *Planorbis cathcarti*).
Gyraulus meridionalis - Smith & Kershaw, 1981: 125, distribution map 28 (samples from Great Lake).
Planorbis atkinsoni Johnston,1879 - May, 1921a: pl. 10, fig. 10 (non Johnston, 1879); 1923: pl. 41, fig. 16 (non Johnston, 1879).
Glyptanisus atkinsoni variant, - Cotton, 1943: pl. 19, figs 3 and 4 (non Johnston, 1879).
Glyptaniscus [sic] *atkinsoni* - May & Macpherson, 1958:
Planorbis cathcarti Petterd, 1889 [nomen nudum] - Iredale, 1943: 225 under *Glyptanisus meridionalis*. Although Iredale here cites Petterd, 1889, pl. 1, figs 4-6, that publication gives no indication that Petterd intended to figure this taxon. Under *P. cathcarti*, Iredale also cites May, 1921a, 70, pl. 10, fig. 11, but May does not refer to this taxon; - Smith, 1992: 277, under species incertae sedis.

Type materials: Holotype; QVM:9:7857, Tasmania, Great Lake, March 1891, ex Simson collection, originally labelled *Planorbis tasmanicus*. Paratypes: QVM:9:7857 (11 dry) and QVM:9:7862 (3 dry), Tasmania, Great Lake, March 1891, ex Simson collection, originally labelled *P. atkinsoni*; BMNH 93.32.378-83 (6 dry), Tasmania, Great Lake, J.H. Ponsonby.

Additional materials examined:
BMNH 96.11.49-50 (2 dry). Tasmania, labelled "*Planorbis cathcarti* Petterd"; bought of G.W. Sowerby, according to Register. QVM:9:7855 (3 dry). Great Lake, without other data; ex Petterd collection. QVM:9:7856 (2 dry). Great Lake, without other data; ex Petterd collection, originally labelled *Planorbis cathcarti*. QVM:9:7858 (2 dry). Great Lake; without other data. QVM:9:7860 (2 dry). Great Lake, without other data; ex Petterd collection, originally labelled *P. atkinsoni*. MV F79276 (1 dry). Great Lake, ex C.J. Gabriel Collection, 29.8.63, "in exchange from Adelaide Museum, 15.4.35", labelled *P. atkinsoni*. TMH E878/8219 (1 dry). Great Lake, ex W.L. May collection, labelled *Glyptanisus atkinsoni*). TMH E2394/17689 (2 wet). Great Lake, April 1939, coll. J.W. Evans.

Diagnosis: A *Gyraulus* which differs from all known species from Tasmania, mainland Australia and continental south and east Asia in its comparatively high and angular whorls.

Derivation of name: After Miena (pronounced My-ee-nah), aboriginal place-name on the southern shore of Great Lake.

Description of shell (Figs 5,6,7,16G-L, Table 2): Holotype (Fig 16G,H,I) nearly planispiral, with an angle on the periphery at about mid-whorl, subangular on the left side, which is deeply concave. Within the subangle on the last half whorl

the surface is first flat or slightly concave and then slopes steeply to the suture. Whorls 3.8 (Fig. 5), the last one high in proportion to its breadth; a/b, 2.82 (Fig 6); depression angle, 76° (Fig. 7). Right side with the earliest 2.5 whorls sunken; no definite angle on this side, but the last whorl is steeply curved near the suture and slopes almost flatly to the periphery. Aperture obliquely pentagonal. Sculpture of numerous close-set collabral ridges of varying strength, the stronger ones spaced nearly regularly; no spiral pattern evident. Colour pale yellowish-brown.

Some paratypes are more definitely subangular on the right side than is the holotype, and are more angular on the left side. The proportional height of the last whorl may be even greater: minimum a/b about 2.3 (Figs 6, 16K); depression angle reaching 91° (Fig. 7). Some paratypes have the last whorl more deflected than the holotype, so that they are more deeply concave on the left side and the right side is more domed (Fig.16K). Colour of paratypes, pale yellowish to greenish brown.

All the shells seen from Great Lake were medium-sized to large, the smallest intact specimen being about 4mm in diameter; the largest, allowing for the damaged lip, had reached nearly 6mm. In comparison with the type series, some of the other shells were rather more depressed and more distinctly keeled at the periphery (MV F79276 and TMH E2394; a/b to 3.3). Spiral striae were present, though weak and confined to the right side, in some shells in two lots (MV F79276 and QVM:9:7860). Like some of the paratypes many of the other shells examined had the lip severely damaged, suggesting that the snails might have lived in agitated water on a wave-washed shore. The two shells in BMNH labelled "*P. cathcarti*" and "Tasmania", without any further detail of locality, are of the same form.

Dimensions:

	whorls	diameter	a	b	a/b
Holotype	3.80	5.64	3.89	1.38	2.82
Paratypes					
QVM:9:7857; only those with lip complete enough for accurate measurement of diameter					
	3.29	4.11	2.80	1.20	2.33
	3.50	5.35	3.89	1.49	2.61
QVM:9:7862; the two least damaged shells					
	3.48	4.80	3.27	1.27	2.57
	3.29	4.55	3.20	1.35	2.37
BMNH 93.3.2.378-383; largest and smallest undamaged shells					
	3.78	5.27	3.67	1.52	2.41
	3.47	4.55	3.31	1.27	2.61

Anatomy: Visible through the shells of some paratypes of *G. mienanus* sp.n. were the remains of the dried body, which apparently had a darkly pigmented mantle roof. Since the body of the single specimen available for dissection (THM E2394) was in contrast pale, and as its shell was comparatively depressed, the

conspecificity between this snail and the type material is not beyond doubt (see further under Remarks). This body was much contracted and poorly preserved; no pigmentation was evident apart from weak eye-spots. Kidney margins much folded through contraction, but apparently not septate. Intestine with long posterior loop extending beyond the stomach. Copulatory organ like that of *G. meridionalis;* vas deferens inserted a little subterminally on the penis sheath, penis attached at nearly one-third of the distance from the top of the sheath towards the preputium, penis tip swollen, penis pore close to base of stylet. Bursa copulatrix of club spherical shape. Seminal vesicle with about 7 spinous convolutions. Ovotestis lobes about 8 only. Prostate too poorly preserved for description; the radula disintegrated during preparation.

Comparison with other species: Having whorls that are comparatively high in proportion to their breadth, the shells of *G. mienanus* sp. n. from Great Lake gave low values for a/b , forming a cluster lying below the range for the other species of *Gyraulus* described from Tasmanian shells (Fig. 6). The depression angle is consistently higher than for the other taxa (Fig. 7). Those individuals of the new species that approach most closely to the other taxa, in a/b or in depression angle, were distinguishable by their more deeply concave left side, the angled whorls on this side and the stronger transverse ridges.

The dark pigmentation of the mantle observed within some of the dry paratypes of *G. mienanus* sp. n. was not seen in any other specimens of *Gyraulus* from Tasmania during this study, but as the single dissected animal from Great Lake was pale there may be wide variation in the pigmentation.

The shells of named taxa of *Gyraulus* from the Australian mainland are generally more depressed than *G. mienanus* sp. n. The most similar is *G. hesperus* (Iredale, 1943; type locality: Lennard River, Western Australia), of which the last whorl is comparatively high and the left side may be deeply concave (Brown, unpublished observations on the type material, AMS C100594). However, in *G. mienanus* sp. n. the proportional height of the whorls is even greater, the whorls are more angular and lack the strong spiral sculpture present in *G. hesperus*. Unlike the Tasmanian species, *G. hesperus* is found in rivers, streams and creeks.

G. connollyi Brown & Van Eeden, 1969 of South Africa resembles *G. mienanus* sp. n. in having high whorls and a deeply concave left side, but like *G. hesperus* it lives in rivers and streams, and is not known to occur in a lake. Independent evolution of this form of shell is not surprising as its compactness and strength seem adapted to life in agitated water, whether on a lake lake shore or in a stony stream. Several species of high-whorled pseudodextral planorbids are indeed found in African lakes, and some were originally classified in *Gyraulus,* but all those for which the male genitalia are known have been found to belong to *Ceratophallus* (Brown & Mandahl-Barth, 1973; Brown, 1980, 1994).

From the species of *Gyraulus* known from south and east Asia (Meier-Brook, 1983, 48-66), *G. mienanus* sp.n. can be distinguished by the greater proportional height of its whorls and the presence of an angle or a subangle above and/or below the peripheral angle. The penis, known from only a single specimen, was attached distantly from the proximal end of the penis sheath,

instead of close to it as in those Asian species for which the structure is known (*G. convexiusculus* (Hutton) (Brown, 1981, fig. 4); *G. malayensis* Meier-Brook, 1983, fig. 91c).

G. mienanus sp.n. shows resemblances, as one would expect, to other species from old lakes (Hubendick & Radoman, 1959; Meier-Brook, 1983). Characteristics of such species are the evolution of marked pseudodextrality, sometimes with development of a distinct spire, and formation of spiral angles on the whorls. Such similarities between species living in different lakes are due to convergent evolution rather than to common origin (see discussions in Meier-Brook, 1983 and Gorthner, 1992). *G. mienanus* sp.n. can be distinguished from these species as follows:

Gyraulus lychnidicus Hesse, 1928, from Lake Ochrid differs in having a higher spire and stronger angulation.

G. trapezoides Polinski, 1929, from Lake Ochrid differs in being more sharply angular and varying in shape from planispiral to high-spired.

G. albidus Radoman, 1953, from Lake Ochrid differs in its more depressed and non-angular shell.

G. crenophilus Hubendick & Radoman, 1959, from spring-fed streams near Lake Ochrid differs in its higher spire and lack of angulation.

G. fontinalis Hubendick & Radoman, 1959, from a small lake near Lake Ochrid differs in having the body whorl more or less keeled both above and below.

G. stankovici Hadzisce, 1953, from Lake Prespa differs in having a more depressed shell, with three strong keels.

G. biwaensis (Preston, 1916) from Lake Biwa, Japan, has a shell of similar general form, but with even higher whorls, a smaller umbilicus and additional spiral striae between the angles.

In all the species from Lake Ochrid basin the penis appears to be attached close to the proximal end of the penis sheath (figures in Hubendick & Radoman, 1959, and for *G. lychnidicus* in Meier-Brook, 1983).

Remarks: Specimens of *G. mienanus* sp.n. have been known for over a century, but they were confused with both *G. meridionalis* and *G. atkinsoni*. First Petterd (1889) figured as an example of *Planorbis meridionalis* a shell that apparently is of *G. mienanus* sp. n. (see under *G. meridionalis*, herein), and gave Great Lake and Upper Ouse River as the localities for *meridionalis*. Petterd seems to have been aware that shells from Great Lake were unusual, since he cites in synonymy "*Planorbis cathcarti* mihi M.S"; this name and Great Lake are on an original label accompanying two shells from Petterd's collection (QVM:9:5856) that certainly belong to the new species. The name *cathcarti* is apparently a nomen nudum, which although cited as a junior synonym of *Glyptanisus meridionalis* (Brazier) by Iredale (1943, as *Planorbis cathcarti* Petterd), does not seem thereby to have been adopted as the name of a taxon (see ICZN Article 11(e)). It seems unlikely that Iredale had seen any specimen from Great Lake, for had he done so he would undoubtedly have considered it to be a distinct species. Perhaps Iredale was misled by one of the figures he cites (May, 1921a, pl. 10, fig. 11), which shows a comparatively depressed shell (possibly in QVM:9:116, see under *G. meridionalis*). *P. cathcarti* was listed under species incertae sedis by Smith (1992).

Another shell from Petterd's collection was figured as an example of *Planorbis atkinsoni* by May (1921a, fig. 10); this resembles *G. mienanus* sp.n., and possibly represents one of the shells in lot QVM:9:7860 (see also under *atkinsoni* herein). The same figure was reproduced by May (1923) and May & Macpherson (1958, as *atkinsoni*). Another shell resembling *G. mienanus* sp. n. and from Great Lake was figured as a variant of *Glyptanisus atkinsoni* by Cotton (1943; locality given on his p. 148).

The most recently collected specimens of *Gyraulus* from Great Lake seen in this study were two obtained in 1939 (TMH E2394). Though badly damaged, these evidently were considerably more depressed than the types of *G. mienanus* sp. n., yet the presence of two angles (peripheral and adapertural) and strong collabral ridges seem to justify placing them in the same taxon. Doubt remains, however, since the one body available lacked pigmentation, in sharp contrast to the darkly pigmented mantle visible within some of the dry paratypes.

It is desirable that further collections of *Gyraulus* should be made in Great Lake in order to determine the distribution and ecology of populations, and to obtain a more satisfactory knowledge of the soft parts and variation in shell form.

Gyraulus sp.
(Figs 6, 7, 17A-C, Table 2)

Material examined: AMS C314276 (44 wet). Lake Sorell, near conservation area; 42° 4.6′S, 147° 12.1′E; alt. 820m; on weed, 3 Feb 1987, station TA16, W.F. Ponder and G.A. Clark.

Shell (Figs 6, 7, 17A-C, Table 2): Smaller than *G. mienanus* sp.n. and generally less angular, but similar in the proportional height of the whorl and deeply concave left side. Some specimens with a distinct peripheral angle, though without keel or fringe, but more commonly the periphery is evenly curved or rather flattened and the peristome rounded. A further difference is the presence on some shells of strong spiral striae, dividing the collabral ridges into rows of riblets.

Dimensions of largest shell: whorls, 3.31; maximum diameter, 3.24mm; a, 2.33mm; b, 0.78mm; a/b, 2.98.

Since the largest shells seen from Lake Sorell were only about 3mm diameter, they may not have been fully grown. Although none was so large as the smallest intact specimen available of *G. mienanus* sp.n. (about 4mm diameter and 3.2 whorls), the number of whorls completed by *Gyraulus* sp. was about the same, suggesting that larger shells would have a significantly greater number of whorls than *G. mienanus* sp. n. Large specimens of *Gyraulus* sp. are more depressed, having higher values for the flatness index (a/b) (Fig. 6), than would be expected in *G. mienanus* at the same size, but still much less depressed than the other taxa included in Fig. 6.

Anatomy: Characters of *Gyraulus* sp. are compared with other taxa in Table 3. Three of the larger snails from Lake Sorell were dissected. Dark pigment was

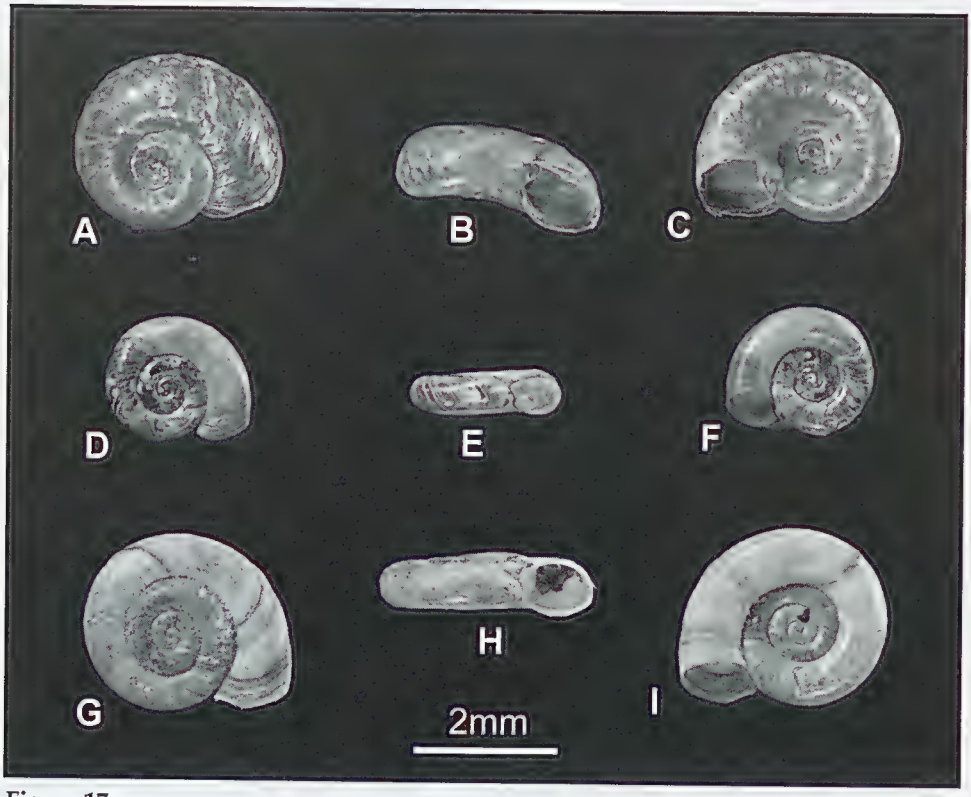

Figure 17.
Shells of *Gyraulus*. **A,B,C;** *Gyraulus* sp.from Lake Sorell. **D-I;** *G. scottianus*. **D,E,F;** from Lagoon of Islands (TMH E12333). **G,H,I;** from Redlands Lagoon (TMH E9991).

absent, apart from weak eyespots, from these and all other specimens in the sample, so far as could be observed through the translucent shell. Kidney margins straight. Intestine either with or without a posterior loop. Copulatory organ and attachment of penis as in *G. meridionalis*. Prostate lobes 7 to 10; probably all on a separate duct though this was not entirely detachable from the sperm duct by dissection. Bursa copulatrix club-elongate or tapering. Seminal vesicle with about 6 spinous convolutions. Ovotestis of about 12 lobes. Radula (2, from snails of shell diameter 3.2mm); formula 19-1-19 and 20-1-20, maximum dimensions of ribbon 1.0 x 0.18mm, number of transverse rows about 150. Central tooth bicuspid; inner lateral teeth (1 to 5) tricuspid, with the endocone very small and the mesocone about twice as long as the ectocone; from about the sixth lateral tooth outwards the endocone increases in size becoming as large as the ectocone; and one or two small additional cusps appear on the lateral side of teeth near the margin.

Remarks: The shell of *Gyraulus* sp. from Lake Sorell, like that of *G. mienanus* sp. n., is separated from the shells of other Tasmanian taxa, by its comparatively small values for the flatness index (a/b) (Fig. 6). If small specimens of *G. meridionalis* were available, it seems likely that their a/b values would converge with those of *Gyraulus* sp., but the latter would probably be distinguishable by their more evenly curved periphery and the rounded lip.

The shell form of *Gyraulus* sp. is apparently related to lacustrine conditions, though modified to a lesser degree than in *G. mienanus* sp.n. To lacustrine influence could also be attributed the small size of the endocone and ectocone on the inner lateral teeth of the radula, since unicuspid teeth are characteristic of several species of *Gyraulus* endemic to Lake Ochrid (Hubendick & Radoman, 1959).

This form of *Gyraulus* from Lake Sorell is perhaps not a distinct species, but rather than unite it with *G. mienanus* sp. n. with considerable doubt, it seems better to present a separate description, as this may encourage further evaluation of these taxa, based on more extensive materials from the Tasmanian highland lakes.

Subgenus **Pygmanisus** Iredale, 1943

Genus *Pygmanisus* Iredale, 1943: 224.
Type species: Planorbis scottiana Johnston, 1879, by original designation.

Shell small, less than 4mm in diameter, with rounded whorls; kidney with undulate margins, septate. Similar in these respects to *Gyraulus* subgenus *Torquis* Dall, 1905, which is found in North America and Eurasia (Meier-Brook, 1983).

Gyraulus scottianus (Johnston, 1879)
(Figs 8,9,10, 12, 15, 17D-I, 18A,B, 19)

Planorbis scottiana Johnston, 1879: 26; - Tate & Brazier, 1882: 559; - Johnston, 1889: 86, fig. 2a-c of second series of figures between pp 86 and 87; - Petterd, 1889: 68 (in account of *P. tasmanicus*); - Johnston, 1891: 145; - May, 1921a: 70, pl. 10, fig. 12; 1921b: 90: 1923, pl. 41, fig. 18; - Gabriel, 1939: 122, pl. 3, figs. 28, 28a and 28b.
Pygmanisus scottianus - Iredale, 1943: 224; - Cotton, 1943: 148; - Smith, 1992: 272.
Pygmaniscus [sic] *scottianus* - May & Macpherson, 1958: pl. 41, fig. 18.
Gyraulus scottianus - Smith & Kershaw, 1979: 87 including fig., 262; 1981: 60 including fig., 125 (distribution map).

Original description: "Shell discoidal, very minute, thin, pale horny, somewhat flattened above and below; whorls 4, depressedly rounded, finely transversely striated, regularly increasing; suture moderately sunk; aperture obliquely raised, roundly lunate; peristome simple. Diam. max. 2½mil., min. 2mil., height ½mil. Habitat, restricted to the same isolated lagoon in which *Gundlachia petterdi* is found"["a pool, 1st Basin, Launceston; isolated from the South Esk.", p. 24 of same paper].

Type material examined: SAMA D16180, 1 syntype, with old label "R.M.J. coll., co-type".

Other materials examined:
AMS C144852 (1 wet). Brown Marsh Creek at Lyell Hwy, small slow-flowing stream, mostly gravel base, 26 Jan 1982; stn TA1687, W.F. Ponder, W.F. Ponder jun. and J. Hall. AMS C314275 (300, wet). Carrie's Brook, E of Maurice Road, 2.5km S of Ringarooma; on dead leaves, roots of willow tree; 41°18.967′S, 147°41.283′E; alt. 260m; 28 Jan 1987, stn TA82, W.F. Ponder, J.H. Waterhouse and G.A. Clark. TMH E9988 (13 wet). Lawrenny, Ouse; irrigation ditch by main

road; 1 Jan 1965, B.C. Mollison. QVM:9:7875 (55 dry). South Esk River, ex Petterd collection. QVM:9:7576 (5 dry). Circular Head. TMH E880 (14 dry). First Basin, Launceston. TMH E 9991 (83 wet). Redlands lagoon, 5 Jan 1965, B.C. Mollison. TMH E12333 (23 wet). Specimens segregated from *G. meridionalis* by DSB. Lagoon of Islands, in fine submerged weed near the shore; 30 Jan 1965, B.C. Mollison.

Shell (Figs 8,9,10,17D-I,18A,B; Table 2): The single syntype seen (Fig. 18A,B) was considered to be too fragile to be subjected to photography. It was nearly 2.2 mm in diameter with 3 whorls (Fig. 8), depressed (a/b, 3.61, Fig. 8; depression angle 65°); with the whorls increasing regularly, entirely curved and not at all angular, rounded at the periphery. Peristome badly damaged; the outer lip was probably rounded. Both sides of shell flat apart from the deflection of the last one-eighth whorl. Transverse ridges weak and irregular; spiral sculpture lacking.

The other shells examined resembled the syntype in shape and rate of increase of the whorls. A few were considerably larger; maximum diameter 3.1 mm, with 3.7 whorls (Redlands Lagoon, TMH E9991). Deflection of the last whorl varied and some shells were entirely planispiral. In many specimens as in the syntype no spiral sculpture was detectable, but some shells had fine striae, though weak in comparison with *G. meridionalis* and hardly deep enough to interrupt the collabral ridges. The whorls became increasingly depressed with growth of the shell; a/b increasing from 2.5 at diameter 1.5mm to 3.8 at diameter 3.1mm. For the most depressed specimen (Lawrenny, TMH E9988) a/b was 4.1 at diameter 2.7mm.

Anatomy (Figs. 12, 15, 18, 19): Description based on 13 specimens from 4 samples: AMS C144852, 1; TMH E9988, 3; TMH E9991, 4; TMH E12333, 5. A few of these contained larval trematodes, which had damaged some organs. Pigmentation (Fig.18C) generally diffuse and weak, practically lacking from left side of mantle roof, right side with greyish band along front margin, greyish black above uterus and along sides of kidney. No specimens had melanin concentrated around the stomach or intestine, where it is commonly conspicuous in *G. meridionalis*. Intestine either with a posterior loop (Fig. 18E), extending back to the crop, in three samples) or without (all 3 specimens from Lawrenny, TMH E9988). Kidney (Fig. 15C-F) septate (confirmed for material from Lagoon of Islands by Dr C. Meier-Brook, in litt. October 1996). Ovotestis with 6 to 11 lobes, in approximately two rows (mean 7.9, n=10). Seminal vesicle (Fig. 18D) only weakly papillate, not at all convoluted. Prostate gland variable even among animals of similar large size (in which no parasites were detected); represented by merely a thickening of the male duct in some specimens, while others had two or three small fingerlike lobes, and one had 6 lobes (Fig. 18D). Copulatory organ (Figs 12D,E; 18D,F-J; 19) reaching about 1.0mm long in some snails of diameter 2.5mm; in other specimens of similar size this organ was much smaller and two were apparently aphallic. This variation in the copulatory organ was possibly related to undetected parasitic infection. In fully developed copulatory organs the penis sheath was about twice the length of the preputium; vas deferens inserted terminally on the sheath. Penis (Fig. 19)

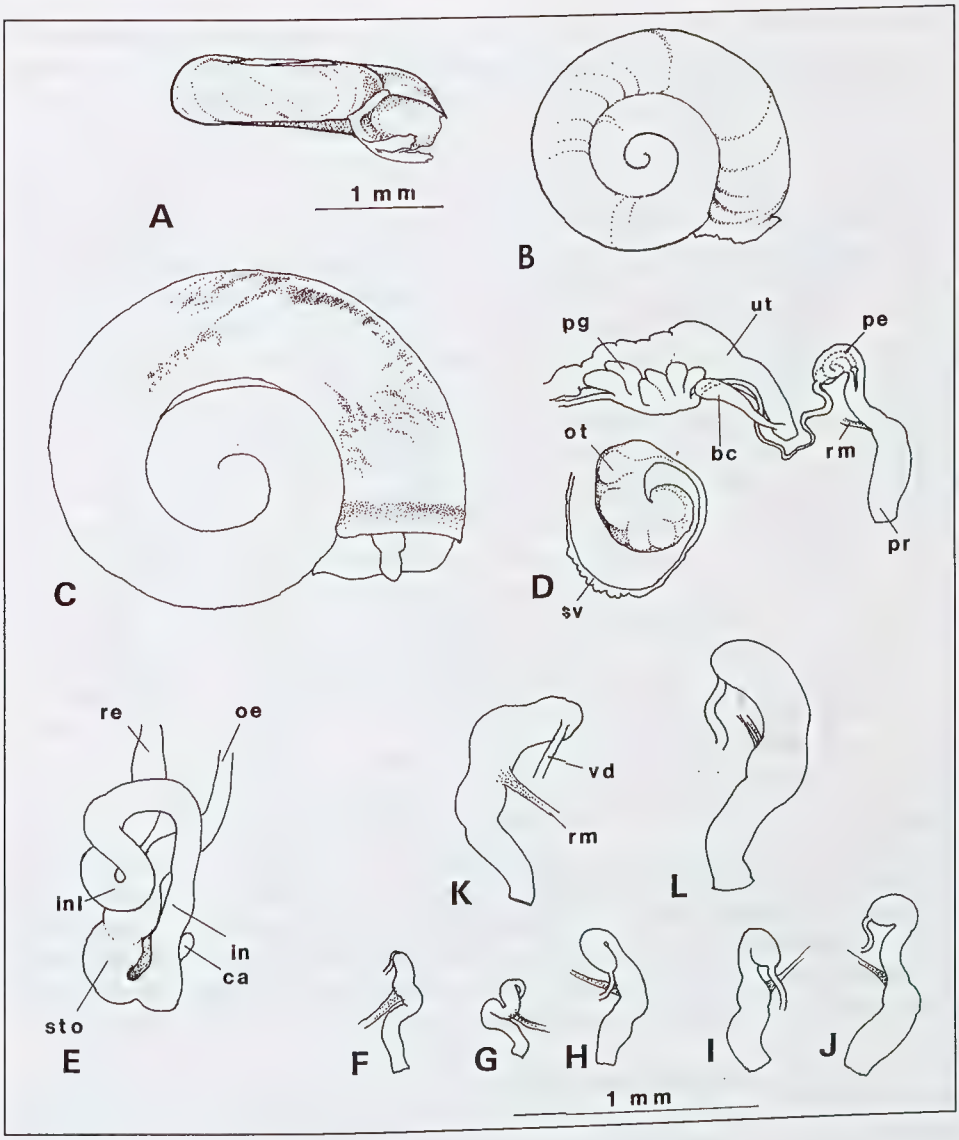

Figure 18.
A-J, *Gyraulus scottianus.* **A,B;** syntype shell (SAMA D16180). **C,D,E;** from Lagoon of Islands. **C,** pigmentation on mantle roof viewed from right side. **D,** genital organs viewed from right side (carrefour region not shown). **E,** intestine, with posterior loop. **F,G,H;** copulatory organs of three specimens from Redlands Lagoon of shell diameters 2.9mm (F), 2.6mm (G) and 2.8mm (H). **I,J;** copulatory organs of two specimens from Lawrenny, of shell diameters 2.7mm (I) and 2.4mm (J). **K,L;** *G. meridionalis.* Copulatory organs of two specimens from Lagoon of Islands, both of shell diameter 2.6mm. Labelling: **bc,** bursa copulatrix. **ca,** caecum. **in,** intestine. **in l,** intestinal loop. **oe,** oesophagous. **ot,** ovotestis. **pe,** penis (seen through wall of sheath). **pg,** prostate gland lobes. **pr,** preputium. **re,** rectum. **rm,** retractor muscle. **sto,** stomach. **sv,** seminal vesicle. **ut,** uterus. **vd,** vas deferens.

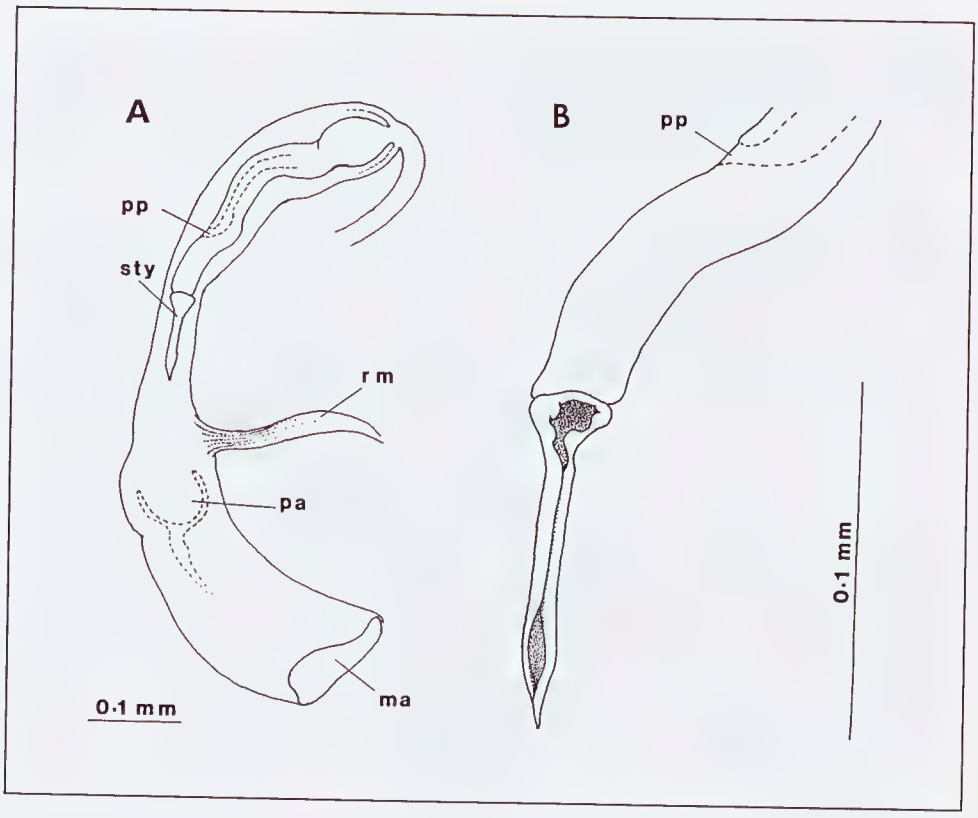

Figure 19.
Gyraulus scottianus. **A,** copulatory organ of specimen from Lawrenny (TMH E9988), drawn to scale from permanent mount, the penis and papilla as seen through the translucent walls of the penis sheath and preputium. Same specimen as shown in Fig. 12D, image reversed here. **B,** penis tip and stylet of specimen shown in (A). No groove between the penis pore and the base of the stylet could be seen. Labelling: **ma,** male aperture. **pa,** papilla. **pp,** penis pore. **rm,** retractor muscle. **sty,** stylet.

slender, sometimes coiled in the bulbous upper part of the sheath. Base of penis attached at the proximal end of the sheath, not at some distance towards the preputium as in *G. meridionalis*. Penis tip (Fig. 19) without distinct swelling; penis pore subterminal. Penial stylet attached terminally, about 0.1mm long, of the dagger-like type with bulbous base and furled blade, as in *G. meridionalis*. Stylet (Figs 12E, 19B) observed in specimens from all localities except those from Lagoon of Islands, of which none seemed mature. Bursa copulatrix (Fig. 18D) generally slender, mostly tapering or elongate club-shaped, but in one specimen approaching the spherical tadpole shape. Radula (5 from snails of diameters 2.0 to 2.8mm); formula 13-1-13 or 14-1-14, excluding one or two cuspless rudiments at margins; maximum dimensions of ribbon, 0.5 X 0.1mm; number of transverse rows of mature teeth from 120 to about 155.

Comparison with other species: G. scottianus may be distinguished from *G. meridionalis* by its smaller size, rounded periphery and, at a given diameter,

the somewhat greater number of its whorls, which expand less rapidly than in *meridionalis*. According to these criteria, the originally mixed sample from Lagoon of Islands (TMH E12333) was readily divisible into these two taxa.

The somewhat larger specimens of *scottiana* from Redlands Lagoon (TMH E9991) extended the size range available for comparison. Some large shells of *scottianus* had completed about half a whorl more than *meridionalis* of similar diameter (Fig. 8). The two species were similarly depressed and the distribution of (a/b) for *scottianus* coincided closely with that for *meridionalis* in the lower half of its size range (Fig. 9), but *meridionalis* was more or less angular over its entire size range including the smallest shells (Fig. 10). In its soft parts (Table 3) *scottianus* differed in the lack of melanin around the stomach and intestine, the presence of septa in the kidney, the lack of both convolution and spinous projections in the seminal vesicle, and the lesser development of prostate lobes. Differences in the copulatory organ of *scottianus* included its smaller size at a similar shell diameter (Fig. 18F-L), the insertion of the vas deferens terminally on the penis sheath, the comparatively long and slender penis and the lack of swelling at its tip. Though smaller, the penial stylet is of the same form as in *meridionalis* and therefore not of the "hobnail" type described by Meier-Brook (1983) for some other small species of *Gyraulus*.

Remarks: Although the type material has been presumed lost (Smith, 1992), the status of the syntype in SAMA (Fig. 18A,B) is well supported by the accompanying old label, and reference to a type series by May (1921a, see below) suggests that additional syntypes may be found. The present shell corresponds well to Johnston's description and his crude figure, which shows only 3 whorls rather than the 4 mentioned in his description.

Subsequent authors agree in their concepts of this species. May (1921a, 70) regarded *P. scottiana* as "very distinct from our other species" and figured "Petterd's specimen, compared with the type series"; this figure resembles the syntype in shape (May gave neither dimensions nor a scale). The same figure was reproduced by May (1923) and May & Macpherson (1958). The species was reported to occur at Tarraville in Victoria by Gabriel (1939), who figured a shell like the syntype though showing about one half of a whorl more. Iredale (1943) founded the new genus *Pygmanisus* on *P. scottiana* and considered this species to be widespread in the south-eastern continent, ranging northwards to Armidale in NSW.

Smith & Kershaw (1979, 1981) were the first to place Johnston's *P. scottiana* in *Gyraulus*. They figured a shell that resembles the syntype described here and gave the distribution as widespread in Tasmania generally, Victoria and southern NSW. The occurrence of *G. scottianus* in these areas of mainland Australia is also indicated by my own unpublished observations. Smith (1992) restored *Pygmanisus* to the rank of a distinct genus, but the morphology described here supports its placement as a subgenus within *Gyraulus* (see below under "Classification at levels of genus and species").

Classification at the levels of genus and species

No materials from Tasmania and little from mainland Australia were available

to Meier-Brook (1983), whose taxonomic revision of *Gyraulus* is still the most comprehensive available. The present observations suggest that all the discoid planorbids found in Tasmania belong to *Gyraulus sensu lato*,as this was defined by Brown & Van Eeden (1969) and Meier-Brook (1983, pp.2, 100-101), according to the shell with less than 5 whorls, and the penis with a chitinised dagger-like stylet, clearly distinct from the soft tissue of the penis.

Consideration will now be given to the standing of the two genus-group names founded on Tasmanian species of *Gyraulus*, in relation to the 7 subgenera defined by Meier-Brook (1983).

Plananisus Iredale, 1943, 224.
Original diagnosis: "A second series [after *Pygmanisus*, defined in the preceding sentence] also common in the south is large, whorls still rounded, mouth oblique, but in the same plane almost free, typified by *tasmanicus* Ten-Woods, and which is here called *Plananisus*".
Type species: Planorbis tasmanicus Tenison-Woods, 1876, by original designation.

Other species assigned by Iredale (1943): mccoyi Gabriel, 1939, 122 [nomen nudum]; *isingi* Cotton & Godfrey, 1932, 162; *macquariensis* Smith, 1883, 295.

Plananisus was considered to be a synonym of *Gyraulus* by Brown (1981) according to observations on the shell and anatomy of snails from Victoria, identified as *G. isingi* Cotton & Godfrey, and this synonymy was maintained by Smith (1992). The present observations show, contrary to Iredale's concept of the type species *Planorbis tasmanicus*, that roundness is not a characteristic of its whorls, and this taxon is apparently not distinct from the earlier-named *G. meridionalis*. This species conforms to *Gyraulus sensu stricto* of Meier-Brook (1983, p. 99) in its shell form (planispiral and to a varying degree angular and fringed) and general anatomy. But the distal position of attachment of the penis, at a considerable distance away from the proximal end of the sheath, in *G. meridionalis* (and other species-group taxa described here apart from *G. scottianus*), differs from the proximal position of attachment reported for *Gyraulus* from outside Australia (e.g. Brown & Van Eeden, 1969, fig. 2; Meier-Brook, 1983, fig. 31). Observations on extensive material from mainland Australia (Brown, in prep.) show the penis is attached proximally in many populations, including material representing *G. gilberti* (Fig. 12C), and the distally attached form of penis has been observed only in snails from a few localities in southern Victoria. More extensive investigation of the copulatory organ in *Gyraulus*, on a world-wide scale, is needed to determine whether the distally attached form of penis may define a monophyletic group; if so this could bear the subgeneric name *Plananisus* Iredale.

Pygmanisus Iredale, 1943, 224.
Original diagnosis:"A very small form with rounded whorls and small rounded mouth of southern range".
Type species: Planorbis scottianus Johnston, 1879, by original designation.
Other species assigned by Iredale (1943): *leonatus* Iredale, 1943; *pelorius* Iredale, 1943.

Species assigned by another author: parvus. Cotton, 1943 (*Pygmanisus*).

Brown (1981) pointed out that the Australian planorbids of the *Pygmanisus* group, by virtue of their small size and slowly increasing rounded whorls, are similar to certain planorbid genera characteristic of Africa. However, the present observations on the anatomy of the type species of *Pygmanisus* do not show affinity with these African planorbids; the critical penial morphology conforms to that of *Gyraulus*. Therefore if *Pygmanisus* is to be recognised as a distinct group, it seems preferable to classify it as a subgenus of *Gyraulus* rather than as a distinct genus as did Smith (1992). Among the subgenera of *Gyraulus* defined by Meier-Brook (1983), *G. scottianus* conforms best to *Torquis* Dall, of North America, Europe and western central Asia (Meier-Brook, 1983, fig. 116), in its shell (rounded whorls), stylet (furled and dagger-shaped, rather than hobnail type) and kidney (septate). In addition, the prostate lobes of *G. scottianus* are few and irregular in arrangement, as in some specimens of *G.(T.) parvus* from Europe (Meier-Brook, 1983, fig. 50) and an intestinal loop may be present or absent as observed by Meier-Brook in *G. parvus*. However, this species in North America is reported to have regular prostate lobes and a consistently straight intestine (Jung & Burch, 1990). Although the septate form of kidney is known also in subgenera *Lamorbis* Starobogatov of Europe and *Armiger* Hartmann of the Holarctic region, both these groups differ from *G. scottianus* in having a hobnail stylet, and *Armiger* has an acutely angled shell.

G. scottianus and other Australian taxa with a similar shell (*leonatus, pelorius*) are so distinct from all other species of *Gyraulus* known from Australia that it seems natural to place them in a distinct subgenus. Whether this group should be *Pygmanisus* or *Torquis* is an open question. In favour of *Pygmanisus*, the character combination of small size, rounded whorls and septate kidney could have evolved independently in Australia. Yet the restricted distribution of these snails, known only from south-eastern Australia, would be consistent with the hypothesis that they could be descended from colonising specimens of *G. (Torquis)* introduced since European settlement. This is a question that might be answered by allozyme electrophoresis or molecular sequencing. For the present, since *G. scottianus* clearly does not belong in *Gyraulus s.s.*, it seems preferable to recognise *Pygmanisus* as a subgenus, rather than place *scottianus* in *Torquis* and so foster biogeographical speculation that may be unwarranted.

The classification of species emerging from the present observations is presented in Table 1, which includes for comparison the earlier treatments by Smith & Kershaw (1981) and Smith (1992). To distinguish between *meridionalis* and *tasmanicus*, Smith & Kershaw (1979, 1981) referred to a more sharply angular periphery in the former, but this aspect of shell shape varies continuously, and since no anatomical difference between these two taxa has been observed, they are treated here as conspecific. On the other hand, although *G. atkinsoni* is perhaps no more than a depressed, acutely angled form of *meridionalis*, I prefer to maintain *atkinsoni* as distinct, at least for the present in order to encourage further investigation of this form.

A key question concerning the wider relationships of the *Gyraulus* fauna of Tasmania is whether *G. meridionalis* is conspecific with the earlier-named

Planorbis gilberti of "New Holland" (type locality restricted to Brisbane district by Iredale, 1943). Comparison of type materials suggests that they are different. The 3 syntypes of *gilberti* are comparatively large and high-whorled shells, giving values for the flatness index and depression angle that plot near *G. mienanus* sp. n. rather than *atkinsoni, meridionalis* and *tasmanicus* (Figs 6,7). Even so, *G. mienanus* sp. n. is clearly different from *gilberti* in the generally greater proportional height of its whorl, the stronger development of angulation on the left and right sides of the whorls, the stronger transverse ridges but weaker spiral sculpture, and the deeper concavity of the left side. Since the type specimens of *gilberti* represent probably only a small part of this species' range of variation, and many probably conspecific shells from eastern Queensland and New South Wales have the whorls more depressed than the types (Brown, in prep.), the variation of shell proportions in *gilberti* may well prove to overlap that of *meridionalis*. However, the present observation that the penis of *gilberti* is attached proximally rather than distally as in *meridionalis*, supports treatment of these taxa as different species. Therefore *gilberti* does not appear to be the senior name for any of the species-group taxa of Tasmania.

Discussion

According to the present morphological observations *Gyraulus* is represented in Tasmania by two or perhaps three comparatively widely distributed species and one or two species restricted to highland lakes. Although this diversity is low beside the 47 taxa recently recognised within the Tasmanian freshwater prosobranch genus *Beddomeia* (Hydrobiidae) (Ponder, Clark, Miller & Toluzzi, 1993), it is not out of line with the 10 species of *Gyraulus* known in South and East Asia (Meier-Brook, 1983, 48-66), or the total of only two indigenous species found in tropical Africa (Brown, 1994).

My study of the small discoid planorbids of Australia originated from the interesting biogeographical consideration, that investigation of their anatomy might reveal representatives of genera that are endemic to the Afrotropical region and are distinguished by characters of penial morphology. So far no evidence for vicariant distribution has come to light, and all the Australian specimens examined (Brown, 1981; present paper) have had the penial morphology characteristic of the almost cosmopolitan genus *Gyraulus*. This is so even for *G. scottianus*, whose shell looks remarkably similar to those of the African genera *Afrogyrus* and *Ceratophallus*. These groups are thus probably Afrotropical endemics, but they should still be searched for in Australia, bearing in mind that the ancylid *Burnupia* was long believed to be endemic to Africa, yet it has recently been found in south Brazil, living in numerous localities and apparently indigenous (Lanzer, 1991, 1996).

The description of *G. mienanus* sp. n. from Great Lake adds a further element to the endemic gastropod fauna known from highland lakes in Tasmania (Smith & Kershaw, 1981), i.e. *Glacidorbis pawpela* Smith, 1979 (Hydrobiidae; known only from Great Lake) and *Ancylastrum cummingianus* (Bourguignat, 1854) (Planorbidae; Great Lake and a few other lakes in the central

highlands). The new species follows the trend towards production of a high and multi-angled shell shown by *Gyraulus* in other ancient lakes (Meier-Brook, 1983; Gorthner, 1992). Another lacustrine taxon is recognised here, *Gyraulus* sp. of Lake Sorell, and probably further distinct forms will be found when planorbids have been collected systematically from the many highland lakes in Tasmania.

This morphological study contributes to a better understanding of the species of *Gyraulus* occurring in Tasmania, first by clarifying both the characteristics of previously named taxa and the past usage of their names, and secondly by providing evidence of a radiation of lacustrine taxa in highland lakes. To judge with more confidence the boundaries between biologically valid species, morphological comparisons will have to be supplemented by evidence from molecular genetics, especially to clarify relationships of fundamental importance to taxonomy:

(1) between *G. meridionalis* of Tasmania and *G. gilberti* of mainland Australia,
(2) between *G. scottianus* of Tasmania, the later-named species of *Gyraulus (Pygmanisus)* found on the mainland, and *G. (Torquis)* of North America and Eurasia.

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References

Brazier, J. 1875. Descriptions of eight species of Australian and Tasmanian land and freshwater shells. *Proceedings of the Linnean Society of New South Wales* **1:** 17-20.

Brown, D. S. 1980. *Freshwater snails of Africa and their medical importance.* Taylor and Francis, London.

Brown, D. S. 1981. Observations on Planorbinae from Australia and New Guinea. *Journal of the Malacological Society of Australia* **5:** 67-80.

Brown, D. S. 1994. *Freshwater snails of Africa and their medical importance.* 2nd edition. Taylor and Francis, London.

Brown, D. S. & Mandahl-Barth, G. 1973. Two new genera of Planorbidae from Africa and Madagascar. *Proceedings of the Malacological Society of London* **40:** 287-302.

Brown, D. S. & Van Eeden, J. A. 1969. The molluscan genus *Gyraulus* (Gastropoda: Planorbidae) in southern Africa. *Zoological Journal of the Linnean Society* **48:** 305-331.

Burch, J. B. & Jeong, K. H. 1984. The radular teeth of selected Planorbidae. *Malacological Review* **17:** 67-84.

Clessin, S. 1885. Limnaeiden. *In:* Martini, F. H. W. & Chemnitz, J. H. *Neues systematisches Conchylien-Cabinet etc.* Nuremberg.

Cotton, B. C. 1943. More Australian freshwater shells. *Transactions of the Royal Society of South Australia* **67:** 143-148, pls 14-18.

Cotton, B. C. & Godfrey, F. K. 1932. South Australian shells (including descriptions of new genera and species). *South Australian Naturalist* **13:** 127-167 (Planorbidae on 162-163 and pl. 3).

Gabriel, C. J. 1939. The freshwater Mollusca of Victoria. *Memoirs of the National Museum of Victoria* **11:** 100-139.

Goodfriend, G. A. 1983. Some new methods for morphometric analysis of gastropod shells. *Malacological Review* **16:** 79-86.

Gorthner, A. 1992. Morphology, function and evolution of complex gastropod shells in long-lived lakes. With a contribution to the paleobiology of *Gyraulus multiformis* in the Steinheim basin. *Stuttgarter Beitraege zur Naturkunde Serie B (Geologie und Palaeontologie)* **190:** 1-173.

Hubendick, B. & Radoman, P. 1959. Studies on the *Gyraulus* species of Lake Ochrid. Morphology. *Arkiv for Zoologi, series 2,* **12:** 223-243.

Iredale, T. 1943. A basic list of the freshwater Mollusca of Australia. *Australian Zoologist* **10:** 187-230.

Johnston, R. M. 1879. Further notes on the freshwater shells of Tasmania (with a description of a new species). *Papers and Proceedings of the Royal Society of Tasmania,* **1878:** 19-29.

Johnston, R. M. 1889. Critical observations on recent contributions to our knowledge of the freshwater shells of Tasmania. *Papers and Proceedings of the Royal Society of Tasmania,* **1888:** 84-90 and table.

Johnston, R. M. 1891. Provisional aid to the study of the Tasmanian Mollusca. *Papers and Proceedings of the Royal Society of Tasmania,* **1890:** 57-145.

Jung, Y. & Burch, J. B. 1990. Comparative anatomy and radulae of the *Gyraulus* subgenus *Torquis* in North America (Gastropoda: Planorbidae). *Journal of Medical and Applied Malacology* **2:** 59-77.

Lanzer, R. M. 1991. Duas novas especies de Ancylidae (Gastropoda: Basommatophora) para o Sul do Brasil. *Revista Brasileira de Biologia* **51:** 703-719. (in Portuguese).

Lanzer, R. M. 1996. Ancylidae (Gastropoda: Basommatophora) na America do Sul: sistematica e distribuicao. *Revista Brasileira de Zoologia* **13:** 175-210. (in Portuguese, with English abstract)

Malek, E. A. 1985. *Snail hosts of schistosomiasis and other snail-transmitted diseases in tropical America: a manual.* Pan American Health Organisation, Washington, D.C.

Mandahl-Barth, G. 1958. *Intermediate hosts of Schistosoma.* World Health Organisation, Geneva.

May, W. L. 1921a. A revised census of the Tasmanian fluviatile Mollusca. *Papers and Proceedings of the Royal Society of Tasmania,* **1920:** 65-75, pls 9-12.

May, W. L. 1921b. *A check-list of the Mollusca of Tasmania.* Government Printer, Hobart.

May, W. L. 1923. *An illustrated index of Tasmanian shells.* Supplementary to the check-list issued in 1921. Government Printer, Hobart.

May, W. L. & Macpherson, J. H. 1958. *An illustrated index of Tasmanian shells.* Revised edition. Government Printer, Hobart.

Meier-Brook, C. 1983. Taxonomic studies on *Gyraulus* (Gastropoda: Planorbidae). *Malacologia* **24:** 1-113.

Petterd, W. F. 1889. Contributions for a systematic catalogue of the aquatic shells of Tasmania. *Papers and Proceedings of the Royal Society of Tasmania,* **1888:** 60-83.

Ponder, W. F., Clark, G. A., Miller, A. C. & Toluzzi, A. 1993. On a major radiation of freshwater snails in Tasmania and Eastern Victoria: a preliminary overview of the *Beddomeia* group. *Invertebrate Taxonomy* **7:** 501-750.

Smith, B. J. 1992. Non-marine Mollusca. In: Houston, W. W. K. (ed.). Zoological Catalogue of Australia 8. AGPS, Canberra.

Smith, B. J. & Kershaw, R. C. 1979. *Field Guide to the Non-marine Molluscs of South Eastern Australia.* Australian National University Press, Canberra.

Smith, B.J. & Kershaw, R. C. 1981. *Tasmanian Land and Freshwater Molluscs.* Fauna of Tasmania Handbook no. 5. University of Tasmania, Hobart.

Tate, R. & Brazier, J. 1882. Check list of the freshwater shells of Australia. *Proceedings of the Linnean Society of New South Wales* **6:** 552-569.

Tennison[sic]-Woods, J. E. 1876. On the freshwater shells of Tasmania. *Papers and Proceedings of the Royal Society of Tasmania,* **1875:** 66-83.

Tenison-Woods, J. E. 1879. On some Tasmanian freshwater univalves. *Papers and Proceedings of the Royal Society of Tasmania,* **1878:** 65-72.

Addendum

Additional material

Two shells of *Gyraulus* from Bruny Island (QVM:9:7861; labelled originally Sth Bruni, 1875, ex Simson collection) differ from all other material described here and perhaps represent an undescribed species. Maximum diameter 5.6mm; whorls 3.9, entirely rounded and rather high (a/b 2.9); sculpture coarse, dominated by somewhat nodular spiral ridges, of which about 20 on either side. In order to decide the taxonomic status of these two specimens, it is desirable to study more material of *Gyraulus* from Bruny Island."

Table 1.
Previous classifications of the species of *Gyraulus* found in Tasmania compared with that adopted in this paper.

Smith & Kershaw 1981	Smith 1992	present paper
Gyraulus scottianus	*Pygmanisus scottianus*	*Gyraulus (Pygmanisus) scottianus*
G. tasmanicus	*Gyraulus tasmanicus*	
G. meridionalis	*G. meridionalis*	*G. (Gyraulus) meridionalis* syn. *G. tasmanicus*
	Planorbis atkinsoni [species incertae sedis]	*G. (G.) atkinsoni*
	Planorbis cathcarti [species incertae sedis]	*G. (G.) mienanus* sp.n., from Great Lake syn. *G. cathcarti* nomen nudum
		G. (G.) sp., from Lake Sorell

Table 2.
Statistics for the linear regressions plotted in Figs 5-9 for shell variables of *Gyraulus* : $y = a + bx$

Figure and taxon	a	b	R2
Fig. 5			
atkinsoni	1.7932	0.3801	0.9723
meridionalis	1.7672	0.4020	0.7143
tasmanicus	1.8609	0.3665	0.7195
mienanus	2.3393	0.2232	0.4859
Fig. 6			
atkinsoni	2.0542	0.8079	0.9663
meridionalis	3.5038	0.1504	0.1944
tasmanicus	2.8356	0.3764	0.5388
mienanus	1.4786	0.3472	0.3372
Gyraulus sp.	2.0251	0.3000	0.5723
Fig. 7			
atkinsoni	81.017	-9.4252	0.8568
meridionalis	73.731	-3.5967	0.3775
tasmanicus	92.751	-12.416	0.6445
mienanus	102.24	-6.7201	0.1689
Gyraulus sp.	97.673	-6.3652	0.4183
Fig. 8			
meridionalis	1.7944	0.4685	0.8850
scottianus	1.2580	0.8080	0.9313
Fig. 9			
meridionalis	2.0852	0.7144	0.8480
scottianus	1.3825	1.1234	0.8994

Table 3.
Summary of anatomical data for *G. meridionalis* from Lagoon of Islands (TMH E12333). There are given where appropriate, the mean, standard deviation (SD), range and sample size (n).

Body pigmentation	
mantle roof	weak, lacking distinct pattern (n = 14).
stomach and proximal intestine	grey or black (n = 14).
Kidney	not septate (n = 14).
Intestine	
posterior loop or kink	present (n = 14).
Ovotestis	
number of main lobes	16.3, SD 4.1 , 9-22, n = 10.
Seminal vesicle	convoluted; spinous (n = 10) or smooth (n = 1).
Prostate	
number of lobes	12.3, SD 2.1, 9-15, n = 10.
Copulatory organ	
length, at shell diameter 4.4-5.1mm	1.71mm, SD 0.17, 1.46-1.96, n= 6.
length at shell diameter 2.5-2.6mm	1.15 and 1.22mm (n = 2).
Bursa copulatrix	
numbers of specimens in shape category	club elongate or spherical (3); tadpole elongate (4); tadpole spherical (3).
Radula	
maximum dimensions of ribbon	1.10 x 0.17mm (n = 5).
number of transverse rows	200 approx.
formula	(19-23)-1-(21-23).

Table 4.
Comparative morphology of *Gyraulus meridionalis*, *G. scottianus* and *Gyraulus* sp. from Lake Sorrel.

	meridionalis	*scottianus*	*Gyraulus* sp
Pigmentation			
head-foot: unpigmented (0), greyish (1)	1	1	0
mantle roof: lacking pigment (0), diffusely grey to black without distinct pattern (1)	1	1	0
stomach and intestine: unpigmented (0), grey or black (1)	1	0	0
Kidney			
non-septate (0), septate (1)	0	1	0
Intestine			
posterior loop lacking (0), present (1)	1	0,1	0,1
Genital organs			
ovotestis, number of main lobes: usually less than 10 (0), usually more than 10 (1)	1	0	1
seminal vesicle: straight and only weakly papillate (0), convoluted and spinous (1)	1	0	1
prostate, number of lobes: 6 or fewer (0), 8 to 10 (1), 11 to 15 (2)	2	0	1
penis sheath: vas deferens attached to penis sheath terminally (0) or subterminally (1)	1	0	1
penis attachment in sheath: proximal (0), distal (1)	1	0	1
penis tip: not swollen (0), swollen (1)	1	0	1
bursa copulatrix: tadpole spherical (1), tadpole elongate (2), club spherical (3), club elongate (4), tapering (5)	1,2,3,4	2,4,5	4,5

BOOK REVIEW

***Bivalves of Australia*, Volume 2, 1998.**
Kevin Lamprell & John Healy; Backhuys Publishers, Leiden

Bivalves have been a relatively neglected group of molluscs in contemporary Australian malacological literature. Boasting more than 1400 locally recorded species the Bivalvia are a significant part of the Australian molluscan fauna yet have received comparatively scant attention from popular authors. With the exception of a few families favoured by collectors for their form and colour eg. Pectinidae and Spondylidae, and some commercial groups such as the mussels, oysters and Giant Clams there is a dearth of knowledge about most of the Australian bivalve fauna. Hence the appearance of *'Bivalves of Australia, Vol. 2'* on the booksellers shelves is timely. It is particularly welcomed by those in the malacological fraternity with more eclectic tastes in shells than merely glossy gastropods such as the much published cowries, cones and volutes. Following the publication of the senior author's first volume (with Thora Whitehead), this second volume has been eagerly awaited by amateur collectors and professional malacologists alike. In contrast to volume one which dealt largely with the more popular bivalve groups, this volume includes many of the lesser known families; many with representatives under 5mm (some less than 2mm) in diameter. In the early sixties Bernard Cotton laid the groundwork for a wider review of the Australian bivalves by documenting the impressive southern Australian fauna. Since then trawling expeditions along Australia's eastern and northern coasts have added greatly to the material available for study and provided the impetus for these two publications. However, the senior author's personal efforts in collecting bivalves from many parts of Australia's long coastline over many years should not be underestimated.

Now, for the first time, the bulk of Australia's bivalve fauna is exposed to the general malacological community. Previously much of the information on many of these bivalve families was available only in literature generally not accessible to most collectors. This fact, together with the scattered nature of the scientific literature, has probably also contributed greatly to the lack of taxonomic activity wthin the group. Much of professional malacological research, particularly systematics, is dependent on the widespread collecting efforts of amateurs- 'the feet on the ground, hands in the water people'. In turn their interest is dependent on the availablity of popular literature which provides the names of shells. A primary identification guide such as *'Bivalves of Australia, Vol. 2'* will hopefully stimulate interest, collection and research.

This volume illustrates 707 species from 72 families not covered in volume one. There is also an addendum which presents an additional 71 species from families dealt with in that volume plus a list of corrections to taxonomic placements made in that publication. The colour illustration of most species in the present volume is combined with a reproduction of original line drawings of the smaller representatives in what is an unusual but effective presentation. The original line drawings, in many cases, are of such quality that their depiction of key sculptural features could not have been matched by conventional

photographic methods. In many cases type material was used in the illustrations, largely in acknowledgement of the many misunderstandings which have been perpetrated in the literature through interpretation of often brief and inconclusive descriptions. A significant improvement on the presentation style of volume one is the depection of smaller sized species at the same size (rather than scale) as the larger species. This will add greatly to its utility as an identification guide. The positoning of descriptions and illustrations on facing pages (at the insistence of the authors) is also another practical feature to be commended. In addition there is a useful pictorial guide to families, an interesting introduction covering general aspects of the group and a well researched list of literature references.

The obvious enthusiasm of the senior author has been a major contributing factor to the success of this venture. His knowledge of the Australian bivalve fauna is comprehensive and his eye for new species acute. The scientific and technical skills of John Healy have been widely broadcast through a plethora of beautifully crafted publications. The combination of the qualities possessed by these authors is perhaps not unique in popular natural history publishing, however, in this case it has led to the production of a distinctly unique publication. One which will remain a prime source for students and fanciers of Australian bivalves for many years to come.

Dr John Stanisic
Senior Curator, Malacology
Queensland Museum

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Keen, M. 1969. The Myidae. in: *'Treatise on invertebrate paleontology'*, Part N, Vol. 2 (of 3), pp. N691-692. Mollusca 6, Bivalvia. R.C. Moore (ed.), (Geological Society of America and University of Kansas Press: Lawrence).

Zinsmeister, W.J. 1984. Late Eocene bivalves (Mollusca) from the La Meseta Formation collected during the 1974-75 Joint Argentina-American Expedition to Seymour Island, Antarctic Peninsula. *Journal of Palaeontology* **58(6):** 1497-1527.

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CONTENTS

E.S. Upatham , P. Wangsomnuk , M. Kruatrachue , Y. P. Chitramvong & V. Reutrakul
Acute toxicity of a plant molluscicide, *Brassaia actinophylla* on *Indoplanorbis exustus* and non-target organisms 1

M. Kruatrachue , E. S.Upatham , P. Wangsomnuk , P. Sretarugsa , & Y. Chitramvong
Ultrastructural changes in the digestive system of *Indoplanorbis exustus* (Gastropoda : Planorbidae) exposed to the molluscicides, niclosamide and *Brassaia actinophylla* 15

L. Triantafillos , S. Donnellan & A. J. Butler
Population genetic structure of the muricid gastropod *Lepsiella vinosa* in Gulf St Vincent, South Australia.....31

H.H. Dijkstra & J. Knudsen
Some Pectinoidea (Mollusca: Bivalvia: Propeamussiidae, Pectinidae) of the Red Sea 43

D.S. Brown
Freshwater snails of the genus *Gyraulus* (Planorbidae) in Australia: the taxa of Tasmania 105

Book Review
J.Stanisic
Bivalves of Australia, Volume 2 155